UNIVERSITY OF CALIFORNIA

Santa Barbara

Summer Fog and Live Fuel Moisture in Coastal Californian Shrubland Ecosystems

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Ecology, Evolution and Marine Biology

by

Nathan Charles Emery

Committee in charge:

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September 2016

The dissertation of Nathan C. Emery is approved.

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September 2016

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My committee has been critical for different parts of my dissertation as well as professional development. Max has taught me a lot about being a professional scientist and provided advice on the fire components of my research. Chris has been my go-to fog consultant as well as connecting me to the world of stable isotopes. Dar has guided me through the world of remote sensing and provided quality advice and comments throughout my career at UCSB. In addition to my committee, I have had many unofficial mentors during my dissertation. The Plant Ecology Seminar group, and in particular Bruce Mahall and Josh Schimel made me the scientist, writer and public speaker that I am today. I have also had numerous teaching mentors, especially Tom Even, Lisa Berry and Douglas Bush, who helped me become a better instructor through studying pedagogy and educational research. The CCUT program and an Instructional Improvement Grant were also critical to my success as an instructor. I consider all of my D'Antonio labmates mentors as well. Nicole Molinari, Karen Stahlheber, Alice Levine, Gail Drus, Denise Knapp, Viviane Vincent, Lisa August-Schmidt, Laura Schultheis, Stephanie Ma, Randy Long and Maddie Nolan all were involved in both dialogue, work and fun.

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Emery, N 2016. Writing an Ecology Research Proposal. EcoEDigital Library. Ecological Society of America.
Emery, N and J Lesage*. 2015. Late summer fog use in the drought deciduous shrub, Artemisia californica (Asteraceae). Madroño. 62: 150-157.
Chen, X., **Emery, N**., Garcia, E. S., Hanan, E. J., Hodges, H. E., Martin, T., ... & Tague, C. 2013. Perspectives on disconnects between scientific information and management decisions on post-fire recovery in western US. Environmental management, 1-12.

PUBLICATIONS IN PROGRESS

Emery, N. and A. Swider*. Fog deposition patterns in a coastal shrubland community. *In prep.*

Emery, N. Phenology as a predictor of plant flammability. *In prep*.
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Undergraduate Honors Research: Duke University, Advisor: Justin Wright
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Data Team, NSF Arctic Data Center, National Center for Ecological Synthesis and Analysis (NCEAS), UC Santa Barbara (Summer 2016-present)
ITCE Research-in-Residence at UC Berkeley, University of Utah (Summer 2014)
Isotope Inter-university Training for Continental-scale Ecology Fellowship
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PI's: Carla D'Antonio, Max Moritz, Phil Dennison
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Eastern Oregon Field Ecologist, The Nature Conservancy of Oregon (Summer 2008)
Field Assistant (in Juan Fernandez, Chile), University of Chicago (Winter 2007)
Field Technician, Yellowstone Ecological Research Center (Summer 2007)

TEACHING EXPERIENCE

Instructor of Record, General Plant Ecology, UC Santa Barbara (Winter 2014, 2015, 2016)
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Instructor of Record, Ecology and Management of California Wildlands, UC Santa Barbara (Fall 2015)
- A 24 student field course with weekly field trips to California's ecosystems
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Academic Coordinator, Introductory Biology Lab Course, UC Santa Barbara (Summer 2015)
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- Train and manage eight teaching assistants to teach lab exercises
- Develop lab quizzes, coordinate grading and maintain course website

Teaching Assistant, UC Santa Barbara (2010-2016)
- Introductory Biology Lab Series 1, 2 and 3
- Foundations of Ecosystem Restoration (2012,'13,'14)
- Ecology and Management of California Wildlands
- Introduction to Ecology

Curriculum development for Teaching Assistants, UC Santa Barbara (2012-2013)

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Summer Teaching Institute for Associates, Instructional Development Program, UC Santa Barbara (Summer 2013)

MENTORSHIP

Research Mentor, UCSB (2011-present)

- Mentored three undergraduates through senior thesis projects. One has been published, another is ongoing.
- Involved over 15 other students in my research program

Summer Institute for Math and Science Mentor, UCSB (Summer 2013)

- Mentored four incoming freshmen on an independent research project to demonstrate the scientific method

Jack Kent Cooke Bridges Mentor, UCSB (July 2012)

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SCIENTIFIC PRESENTATIONS

Ecological Society of America: 100th Annual Meeting (Summer 2015)

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American Geophysical Union: Fall Meeting (Fall 2014)

- Poster: Fog Water Use in Coastal California Shrub Species

MEDECOS XIII: Crossing Boundaries across Disciplines and Scales (Fall 2014)

- Talk: Coastal fog effects on live fuel moisture of California shrublands

Ecological Society of America: 99th Annual Meeting (Summer 2014)

- Talk: Foliar uptake and physiology of California shrub species

Mildred Mathias Symposium, UC Natural Reserve System (Spring 2014)

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Ecological Society of America: 98th Annual Meeting (Fall 2012)

- Talk: Fog water use in coastal California shrublands

Ecological Society of America: 97th Annual Meeting (Fall 2012)

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California Native Plant Society Conservation Conference (Winter 2012)

- Talk: How does fog affect fuel moisture?

MEDECOS XII: Linking science with resource management (Fall 2011)

- Poster: How does fog affect the fire regime?

ABSTRACT

Summer Fog and Live Fuel Moisture in Coastal Californian Shrubland Ecosystems

by

Nathan Charles Emery

In semi-arid regions around the world, water availability has a significant impact on plant physiology, plant community dynamics and the functioning of ecosystems. While early research explored the relative effects of rainfall and groundwater on plant and ecosystem processes, recent studies have begun to elucidate the importance of fog on water-limited ecosystems. Along the southern California coast, shrub-dominated plant communities experience seasonal drought simultaneous with coastal fog during the summer months. These plant communities also experience periodic wildfire disturbances due to weather conditions and water limitation. This dissertation sought to address gaps in our knowledge of the effects of coastal fog on shrub water status and live fuel moisture including the potential for wildfires in two shrubland plant associations in Santa Barbara County, California. In the first chapter, I used stable isotopes of hydrogen and oxygen to track fog water uptake and a field manipulation study to exclude fog drip from *Artemisia californica*, a dominant species in the sage scrub association which occurs at low elevations along the California coast. I found that this species takes up fog water during the late summer when conditions are driest and fog is present. I also found that fog drip slightly increases water content in these shrubs, potentially buffering the negative effects of drought. I also detected fog water uptake in the plants that were excluded from fog drip, suggesting water uptake by plant organs other than

roots. This led to an investigation of the potential for foliar water uptake of fog in five common native shrub species which is the basis for chapter two. Chapter Two consisted of a greenhouse experiment in which I exposed shrub leaves to artificial fog over several nights and compared the physiological responses to this treatment with control plants. In addition, one of the nights of exposure included isotopically labeled fog to determine if fog water was taken up by plant leaves. The results suggested that four of the five species tested undergo foliar uptake of fog. Of the species that took up fog water, *Salvia leucophylla* (a drought deciduous species) was affected the most, with treatment individuals having higher water potential and greater photosynthetic capacity than controls. Chapter Three investigated fog water use in a field setting for the same five shrub species from both the chaparral and sage scrub associations. I also attempted to determine the relative influence of fog on live fuel moisture, a metric of plant flammability. The results from this study suggested that all five study species take up fog water during the summer drought, although the lower elevation sage scrub species take up fog in the late summer months due to higher fog deposition compared to the chaparral association. Additionally, the live fuel moisture patterns of the two drought deciduous species, *A. californica* and *S. leucophylla*, were significantly affected by fog deposition over the dry summer months. This dissertation established previously unknown fog water uptake in several dominant shrub species, explored the mechanisms of fog water uptake, and illustrated the importance of fog water availability for plant function and live fuel moisture loss during the summer drought. Overall, these studies established the effects of fog water on dominant shrub species from the chaparral and sage scrub associations of the southern California coast including the potential for fog to influence live fuel moisture drawdown patterns in lower elevation sites.

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ABSTRACT

Coastal fog affects many California plant species and can be critically important to species that experience periodic drought. Drought-deciduous species in particular rely on water availability to maintain their leaves during the summer. To determine fog water use in drought-deciduous plants, this study manipulated access to fog drip and measured the water relations of the common shrub, *Artemisia californica*, near Santa Barbara, CA. Measuring the stable isotope ratio of hydrogen and oxygen, this study found that *A. californica* uses fog water in the late summer months when fog is present. This additional water increased plant water content but had no effect on pre-dawn xylem pressure potential. While climatic variability inhibits reliable fog input to *A. californica* in Santa Barbara, this species can use fog water opportunistically and benefits from large fog events during the summer drought.

INTRODUCTION

In arid ecosystems, water is often the most limiting factor for plant survival and growth. This water generally comes in the form of rainfall; however, in coastal regions fog water can act as a strong influence on plants (Klemm et al. 2012). Fog provides a significant amount of water to plants in regions as distinct as the Atacama Desert of Chile (Cereceda et al. 1999) and Coastal Redwoods of California (Limm et al. 2009). Ecological studies of fog have explored the response of many plant types to fog water inputs (Corbin et al. 2005, Fischer et al. 2009, Limm et al. 2009, Berry and Smith 2012, Vasey et al. 2012, West et al. 2012). However, research has largely ignored drought-deciduous species, whose leaf phenology responds directly to seasonal water availability. Drought-deciduous plants drop their leaves during seasonal periods of drought as a means of conserving water (Harrison et

al. 1971). In coastal California, fog tends to occur in the summer months during peak drought (Williams 2009). This additional water could provide significant physiological benefits for drought-deciduous shrubs along the California coast.

The most common drought-deciduous species along the California coast is *Artemisia californica* Less. (Harrison et al. 1971). This shrub species has high transpiration rates due to weak stomatal control and a thin cuticle (Harrison et al. 1971, Poole and Miller 1975). During periods of summer drought, *A. californica* will shed leaves as a means of reducing water loss. Previous research suggests that the rooting systems of *A. californica* are shallow compared to evergreen species that grow in the same environment (O'Leary 1990). This enables *A. californica* to respond rapidly to rainfall events but also reduces drought tolerance (Poole and Miller 1975). Considering the weak transpirational control and shallow rooting system of *A. californica*, the acquisition of late summer fog could provide significant physiological benefits if the plants are capable of taking up the fog water.

Fog can affect the water budget of *A. californica* through foliar uptake or through fog drip. Fog drip occurs when water vapor from a low-lying cloud condenses on plant material and then drips into the soil where it can be taken up by the roots. Foliar uptake, or the absorption of water into the plant directly through the leaves, can also provide some physiological benefits (Limm et al. 2009), but appears to be short-lived and has yet to be effectively quantified. As *A. californica* is drought-deciduous in the late summer, foliar uptake is unlikely to affect the shrub as there are few leaves for water to enter. However, the shallow rooting system of *A. californica* may allow this species to take advantage of fog drip that collects in the top layer of soil. In this study, we address the question: Can *Artemisia californica* access fog water and if so, does it affect plant water relations? We used the natural abundances of stable isotopes of water extracted from the xylem of the shrubs before

and after fog events to evaluate whether plants could take up fog. Simultaneously, we experimentally excluded fog drip from one set of shrubs using careful placement of tarps. We hypothesized that *A. californica* shrubs exposed to fog drip would experience an increase in their water content and water potential compared to plants from which fog drip was excluded.

METHODS

Study Site

This study was conducted at Coal Oil Point Reserve (COPR), a part of the University of California Natural Reserve System, located approximately two miles west of the University of California Santa Barbara campus in Santa Barbara County, California (34 24'N, 119 52'W). Mean precipitation is 441±8 mm of rain per year with rainfall typically occurring between October and May. Mean temperatures fall between 6°C in January to 24°C in August (UCNRS 2014). This study took place from May to October in 2011 and August to September in 2012. Precipitation data were obtained from the COPR meteorological station (Roberts et al. 2010). Precipitation during the 2010–2011 rain year was higher than average (654 mm of rain), whereas 2012 was a drier year than average (282 mm of rain). Fog was quantified using fog collectors modified from a previous design (Fischer and Still 2007). This study took place in an area with interspersed patches of California sage scrub and grassland. The soil is Concepcion fine sandy loam with intrusions of clay.

Field Sampling

To quantify the effects of fog drip, fog water was excluded from the soil below shrub canopies using plastic tarps in the summers of 2011 and 2012. Fog drip exclusion was done in a manner similar to the precipitation exclusion experiments described in Breshears et al. (2008). In 2011, six adjacent A. californica shrubs were treated by placing tarps from the

base of the stems to several feet beyond the edge of the canopies. The tarps were sealed together with waterproof adhesive tape to form a large rectangular matted area below the six treatment shrubs. The large tarps were removed prior to the first fall rain event in another six adjacent shrubs were left without tarp as control plants. We measured xylem pressure potential (XPP) and plant water content (WC) for each individual shrub. Xylem pressure potential measurements were taken before dawn, between 3:00 and 4:00 a.m. (pre-dawn) and between 1:00 and 3:00 p.m. the next day (midday) on each sampling date. Stem samples were bagged, placed in a cooler and within the hour, measured for XPP in the lab using a Scholander-type pressure chamber (Model 1000, PMS Instrument Comp., Corvallis, OR). Midday XPP stem samples were weighed prior to the XPP measurement and subsequently placed in a drying oven for 48 hours at 80°C. Plant water content was calculated as the water weight divided by the dry weight of the plant tissue. WC samples averaged 2.1 g dry weight (60.58 g). Data was collected monthly from May through October, for a total of six sampling dates.

In 2012, to avoid the problem of pseudoreplication, we selected eight treatment and eight control shrubs that were isolated (.5 m apart) and interspersed with one another in the same area. Tarps were laid underneath treatment shrubs from the stem base to several feet beyond the canopy. Measurements of all plants were taken every two weeks from August through September, for a total of five sampling dates. As in 2011, measurements included XPP and WC. All samples were collected at midday, between 1:00 and 3:00 p.m. At the end of the 2012 field season, 5 cm deep soil samples were taken from below both treatment and control A. californica plants. Cores were collected 5 cm from the base of the plant to measure gravimetric soil moisture content in the lab.

Only adult shrub individuals were selected for the experiment. All shrubs were 0.75–1 m in height and had a large canopy to withstand destructive sampling over a summer season.

Stable Isotopes

To track fog water into xylem tissue, we measured the stable isotopic ratios of hydrogen and oxygen (Dawson et al. 2010). In 2011, we collected water samples from rain, fog and groundwater to characterize the water sources available to A. californica. Each rain event was captured in a small Nalgene container at a location five miles east of the field site. Fog water was collected from a harp-string collector design modified from Fischer et al. (2007) every few weeks during the summer months. Rain and fog water were collected with a 2–3cm layer of mineral oil in the container to prevent evaporation. Ground water samples were taken from nearby wells established by the Cheadle Center for Biological and Ecological Restoration. All water samples were run through a cellulose filter to remove particulate matter before analysis on a Los Gatos Research Liquid Water Isotope Analyzer (Model LWIA-24EP) at the California Institute of Technology.

Multiple fog (44) and rain (19) samples from 2011–2013 were used to construct a local meteoric water line (LMWL). The LMWL for Coal Oil Point Reserve is $\delta D = 7.456\delta^{18}O + 6.4349$, $R^2 = 0.94$. The line differs from the global meteoric water line (Gat 1996); however, this is expected as the line includes water from fog and rain (Gonfiantini and Longinelli 1962). Plant water samples consisted of suberized stem tissue from several of the A. californica shrubs. Once a month in July, August, and September of 2011, plant tissue samples were collected midday in sealed scintillation vials and placed on ice until they were brought back to the lab freezer (-25°C).

Plant water samples were extracted using a cryogenic vacuum extraction line (Ehleringer et al. 2000) at UC Santa Barbara. These water samples were then shipped to the Stable Isotope Biogeochemistry Lab at UC Berkeley where they were analyzed on an Isotope Ratio Mass Spectrometer. Plant water samples were collected in 2012 but were not analyzed, as there was insufficient fog deposition during the summer of 2012.

We corrected all plant water samples for soil evaporation using the correction method developed by Corbin et al. (2005) in Northern California. Use of an evaporation correction is necessary for studies in semi-arid ecosystems, as the water used by plants has experienced evaporative fractionation prior to uptake. Plant samples were corrected back to the local meteoric water line for COPR. We then used a mixing model analysis with two isotopes and three sources (rain, groundwater and fog) for all plant water samples to determine the proportion of fog water used by plants (Phillips and Gregg 2001).

Analysis

Data were analyzed using JMP® Pro 11 (SAS Institute). We conducted a repeated measures analysis for plant water content and predawn XPP over time to compare the effects of the matting treatment within each year. For WC we used a residual error covariance structure as it had the lowest value for the AICc criteria, for five of the six sampling dates (excluding October). For XPP we used an AR(1) covariance structure as it had the lowest value for the AICc criteria. We used a one-way ANOVA to analyze the difference in soil moisture between treatment and control. Differences in fog proportion by date were compared with a pairwise Student's *t* test.

RESULTS

Fog and Rain Inputs

Quantities of rainfall and fog water collected were both greater during 2011 than 2012 (Fig. 1). In 2011, a total of 1693 ml of fog water was collected from 5/6/2011 through 10/25/2011, whereas only 188 ml was collected from 7/1/ 2012 through 9/27/2012. In 2012, fog data collection began two months later than in 2011; however, there was much less late summer fog in 2012. In 2011, total fog collected was more than nine times greater than that of 2012. The only rain event to occur during the treatment period was a 30 mm rain event on 6/6/2011. There was rain on 10/5/2011; however, the tarps had been removed just prior to this event.

The isotopic signature of fog water at Coal Oil Point Reserve was more enriched in the heavy isotopes of Hydrogen and Oxygen compared to both rain and groundwater (Fig. 2) as is typical of fog water in other ecosystems (Scholl et al. 2010). Rain and groundwater were not significantly different from one another.

Fog Water Isotope Analysis

The isotopic signature of A. californica stem water varied across the summer of 2011; it was initially depleted of heavy isotopes in the midsummer and became enriched in September. Both treatment and control plants experienced an increase in the proportion of fog water present in their stem tissue in September. There is a significant difference between September and both July and August (July: $p = 0.0093^*$, August: $p = 0.0008^*$) when treatment and control plants are combined (Fig. 3).

Plant Water Status

In 2011 the plant water content (WC) of both control and fog drip exclusion plants decreased during the summer, and increased after the first fall rain (Fig. 4). A small rain event on June 6th temporarily increased WC of both control and fog drip exclusion plants. A repeated measures analysis of WC for the five sampling dates between June and October

found that there was a significant effect of time ($p < 0.0001$*) with WC generally decreasing throughout the dry season. The treatment effect alone was not significant ($p = 0.4258$), but there was an interaction effect of treatment*time ($p = 0.0004$*). In 2012 the difference in WC between treatment and control was non-significant ($p = 0.2786$) and there was no interaction effect with time ($p = 0.8677$).

The 2011 pre-dawn xylem pressure potential (XPP) of both groups decreased during the summer and increased after the first fall rain event (Fig. 5). A repeated measures analysis of XPP yielded a significant effect of time ($p < 0.0001$*) but no significant effect of treatment ($p = 0.597$). There was no significant interaction effect of the treatment over time ($p = 0.193$). For midday XPP, there was a significant effect of treatment ($p = 0.028$*) as the control plants had slightly higher water potential at each sampling date. This slight difference was observed from the beginning of the experiment as the difference between treatment and control values did not change over time ($p = 0.975$). This indicates that the difference observed was an artifact of the individual plants selected for the experiment, not an effect of the treatment. In 2012 there was no effect of treatment ($p = 0.902$) or treatment over time ($p = 0.340$).

The soil moisture beneath the fog drip exclusion and control plants was significantly different at the end of the 2012 treatment ($p = 0.011$*), with the fog drip exclusion plants having an average soil moisture of 4.66% (±0.66%) and the control plants an average 4.08% (±0.56%).

DISCUSSION

The results presented here support the hypothesis that Artemisia californica uses fog water in the late summer. This additional water appears to increase plant water content for individual A. californica shrubs.

A significant fog event (128 ml over four days) before the September sampling date likely caused the observed difference in WC in September of 2011 (Fig. 4). No rain occurred from August to September, further supporting the idea that the increase in WC of control plants was due to the large fog event that occurred in early September (Fig. 1). While control and treatment plants differed in their WC, the water isotopes in their stem tissue both reflected a higher proportion of fog water in September of 2011 (Fig. 3). This suggests that the treatment plants, despite the attempted exclusion of fog drip, were incorporating fog water into their stem tissue betweenAugust and September of 2011. This presence of fog water in treatment plants, if not through root uptake, may be due to foliar uptake. Foliar uptake of fog has been found in numerous plant species, including California shrub species (Limm et al. 2009). If this is the case, foliar uptake of fog was not enough to alter WC in the treatment plants, but was detected in the water isotopes of all shrubs. For control plants, root access to fog water may have increased WC in September, but it had little effect on the pre-dawn XPP (Fig. 5). These results suggest that although A. californica could acquire fog through multiple mechanisms, root uptake of fog drip can improve the water budget of this drought-deciduous shrub during periods of significant fog deposition.

The similarity in pre-dawn XPP between control and treatment plants may be explained by a difference in soil water content below the tarps. The soil moisture data from 2012 suggests that the tarps had the unintentional effect of reducing soil evaporation, as the control plants had significantly lower soil moisture than the treatment plants. In 2011, this would explain thelack of difference between the XPP of the treatment and control individuals (Fig. 5). If reduction in soil water evaporation increased the amount of water available to treatment plants, it could result in no observable difference in pre-dawn XPP. Alternatively, by the late summer both treatment and control plants may no longer have the

ability to effectively conduct water. The late summer XPP observed in this study is similar to the values observed in Jacobson et al. (2007) where there was 75% loss of hydraulic conductivity in A. californica during the dry season. It is possible that although A. californica can take up fog water, hydraulic conductivity is too low to alter pre-dawn water potential inside stems.

Overall, this study provides the first evidence of fog water use by a drought-deciduous shrub, and attempts to understand the importance of fog drip during the seasonal drought period in coastal southern California. Dropping leaves in the summer is costly for plants and is likely triggered by water availability (Harrison et al. 1971). Fog inputs could prolong leaf lifespan and enablegreater carbon assimilation for species such as A. californica. Our results suggest that fog increases A. californica water content through roots and possibly foliar uptake. However, the effects of fog appear to be temporary and do not provide a consistent summer water resource for coastal California's drought-deciduous shrub species.

The interannual variability of fog deposition observed in this study (Fig. 1) is consistent with long-term cloud records (Williams 2009). In coastal California regions with consistent and large quantities of fog deposition, fog can contribute greatly to plant water relations (Burgess and Dawson 2004, Fischer et al. 2009, Vasey et al. 2012). Plant species in the Santa Barbara region are unlikely to depend on summer fog as a water source, though some may opportunistically use fog water during the summer drought. With predictions of a warmer climate in California (Cayan et al. 2008), the results from this study may provide a window into future climate-plant interactions for more northern shrub-dominated ecosystems along the California coast.

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TABLES AND FIGURES

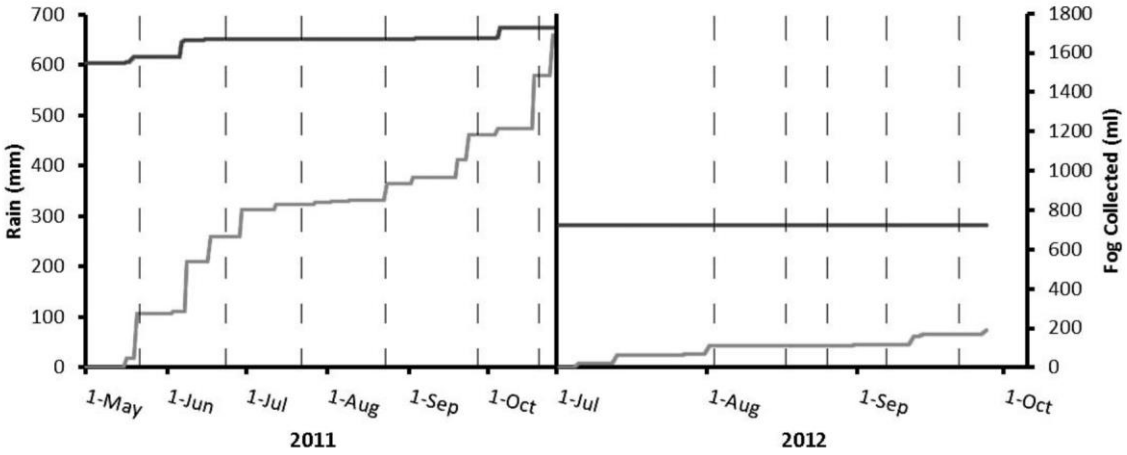

Figure 1. Rain and fog accumulation for 2011 and 2012. The dark gray line represents rain and the light gray line represents fog water. The vertical dashed lines represent the dates of vegetation sampling for each year.

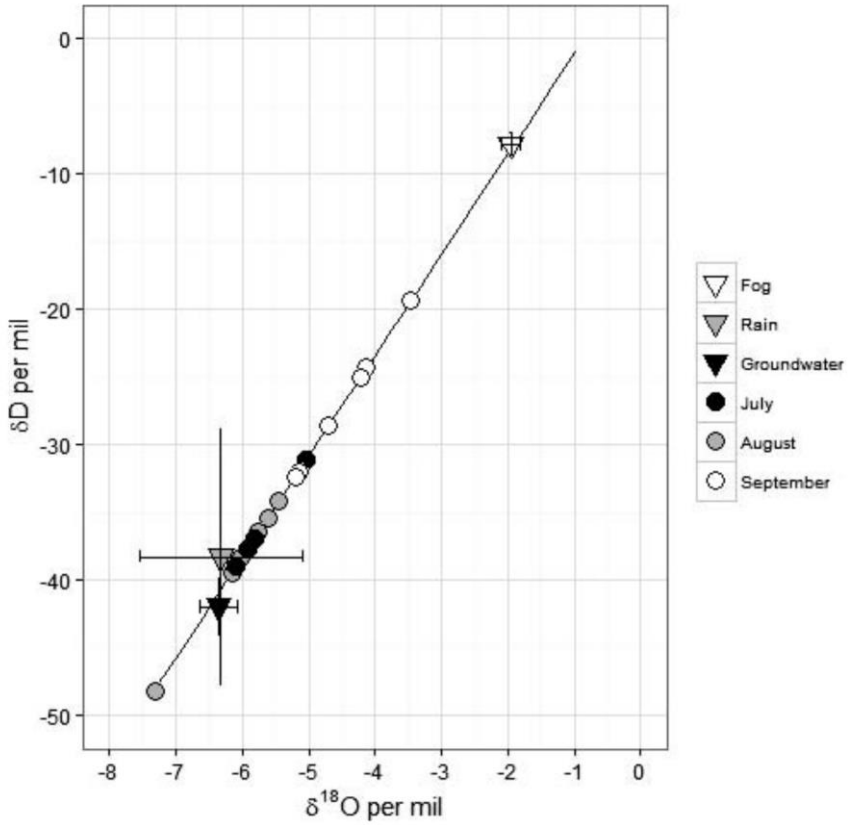

Figure 2. The isotopic signatures of water and *A. californica* stem tissue at Coal Oil Point Reserve. Fog is isotopically enriched in the hydrogen and oxygen isotopes (white triangle). Rain and groundwater are depleted (gray and black triangle, respectively). Plant water samples were corrected to the local meteoric water line (black line). Error bars are the standard error associated with source water isotopic values.

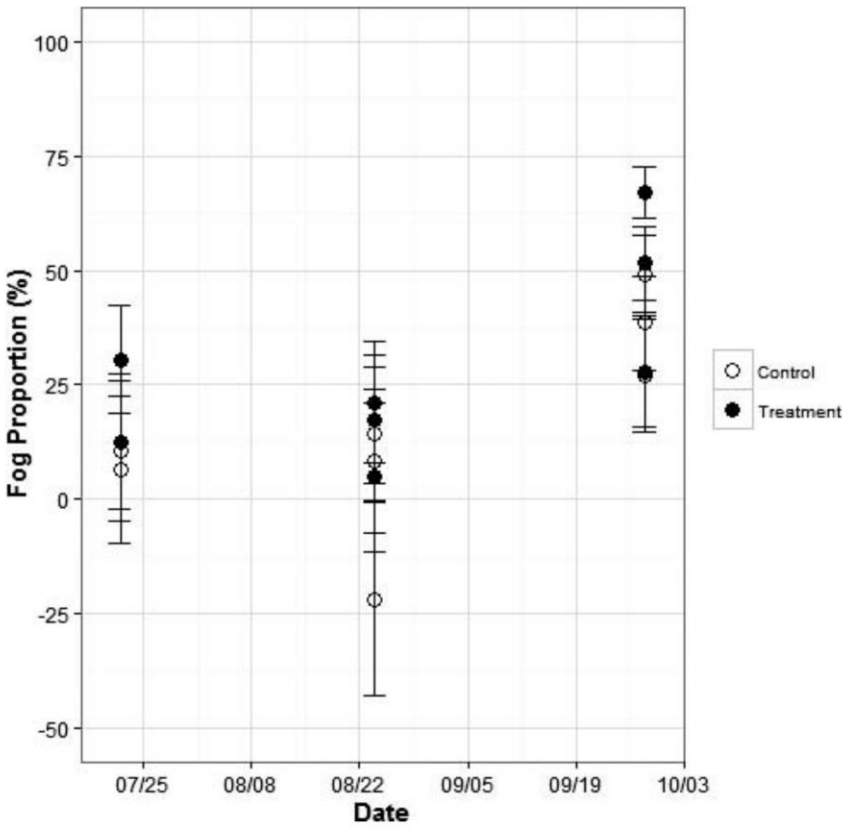

Figure 3. Phillips and Gregg's (2001) mixing model results for fog proportion in stem water for 2011. Both treatment and controls plants shifted towards fog in September. Each point with bars is an individual plant with the mean and standard error of fog proportion according to the model.

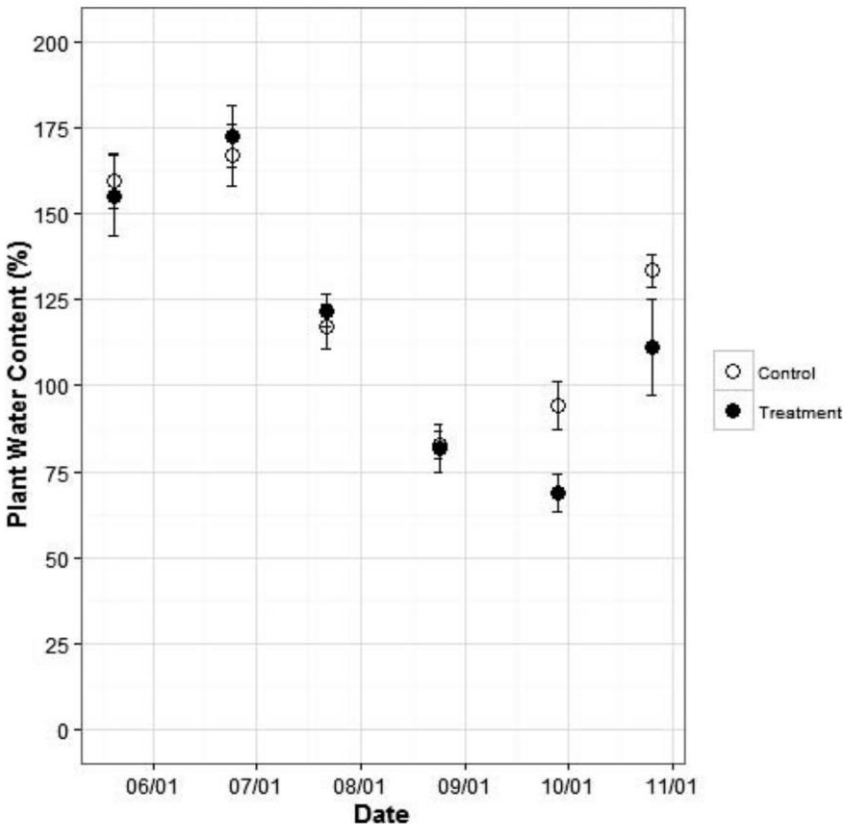

Figure 4. Plant water content (%) of *A. californica* during the 2011 summer sampling period. Error bars represent plus/minus one standard error.

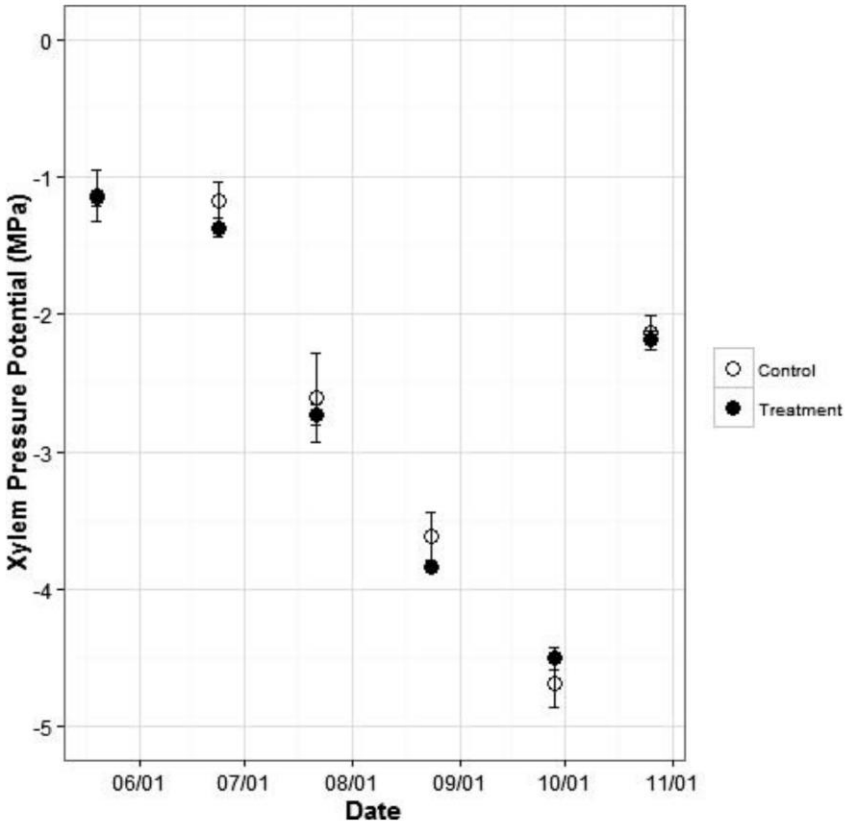

Figure 5. Pre-dawn xylem pressure potential of *A. californica* during the 2011 summer sampling period. Values represent means of the six plants per treatment. Error bars represent plus/minus one standard error.

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Chapter II: Foliar Uptake of Fog in Coastal California Shrub Species

ABSTRACT

Understanding plant water uptake is important in ecosystems that experience periodic drought. In many Mediterranean-type climates like coastal California, plants are subject to significant drought and wildfire disturbance. During the dry summer months, coastal shrub species are often exposed to leaf wetting from overnight fog events. This study sought to determine whether foliar uptake of fog occurs in shrub species and how this uptake affects physiology and fuel condition. In a controlled greenhouse experiment, dominant California shrub species were exposed to isotopically labeled fog water and plant responses were measured. Potted plants were covered at the base to prevent root uptake. The deuterium label was detected in the leaves of four out of five species and in the stems of two of the species. While there was a minimal effect of foliar water uptake on live fuel moisture, several species had lower xylem tension and greater photosynthetic rates after overnight fog treatments, especially *Salvia leucophylla*. Coastal fog may provide a moisture source for many species during the summer drought, but the utilization of this water source may vary based on foliar morphology, phenology and plant water balance. From this study, it appears that drought-deciduous species (*Artemisia californica* and *Salvia leucophylla*) benefit more from overnight fog events than evergreen species (*Adenostoma fasciculatum, Baccharis pilularis* and *Ceanothus megacarpus*). This differential response to fog exposure among California shrub species may affect species distributions and physiological tolerances under future climate scenarios.

INTRODUCTION

Our understanding of plant water uptake has shifted significantly in recent decades. Traditionally, plant physiologists have focused on passive root uptake as the primary means

of water acquisition in plants. The Soil-Plant-Air Continuum (SPAC) framework has dominated the scientific discussion of plant-water movement for many years (Philip 1966). Despite early evidence of water uptake in leaves (Stone 1957), only relatively recently have researchers uncovered the physiological effects and ecological importance of foliar water uptake in plant species (Martin and von Willert 2000, Burgess and Dawson 2004, Breshears et al. 2008, Limm and Dawson 2009, Limm and Dawson 2010, Eller et al. 2013, Berry and Smith 2014, Gotsch et al. 2014). While the mechanism of foliar uptake is not well known, studies have shown uptake through the cuticle (Eller et al. 2013), leaf hydathodes (Martin and von Willert 2000) and stomata (Burkhardt et al. 2012). This uptake can improve water status (Gouvra and Grammatikopoulos 2003, Breshears et al. 2008, Limm et al. 2009, Berry and Smith 2014) and enhance plant survival under drought conditions (Eller et al. 2013). Foliar water uptake influences plant species in a number of ecosystems, and is particularly influential in plant communities with pronounced dry periods (Munné-Bosch 2010, Goldsmith 2013) and episodic leaf wetness (Burgess and Dawson 2004, Breshears et al. 2008, Ewing et al. 2009).

Mediterranean-type climate regions (MTC) are typified by cool, wet winters and hot, dry summers. In addition to seasonal drought, MTCs are influenced by coastal weather patterns. In coastal California, fog forms offshore and is advected onto land by a pressure differential between the coast and the interior of California (Filonczuk et al. 1995). In several coastal California plant communities, fog ameliorates drought stress (Corbin et al. 2005, Fischer et al. 2009, Carbone et al. 2013, Baguskas et al. 2014) and maintains soil water availability (Vasey et al. 2012). Fog events tend to occur overnight and dissipate by mid-morning, exposing plants to foliar wetting that potentially creates a reverse water potential gradient

between the atmosphere and the inside of plant leaves. If water enters the leaves, it could improve plant water status.

For four of the five MTC regions, there are natural fire disturbance regimes that shape plant communities (Edwards 1984, Pausas and Vallejo 1999, Keely and Fotheringham 2001, Bradstock et al. 2002). These fire regimes are characterized by the seasonality, frequency, size, and intensity of fire disturbances within an ecosystem (Whelan 1995). While many climatic and biotic factors affect fire patterns, live fuel moisture, a measure of water content in live plant tissue, is important for ignitability, fire spread, intensity and fire size (Countryman and Dean 1979, Anderson 1982, Dennison and Moritz 2009). While spring rainfall influences LFM patterns in southern California (Dennison and Moritz 2009), it is unknown as to how foliar uptake of summer fog affects live fuel moisture. Foliar water uptake could decrease plant flammability and potentially alter fire patterns. Of the species known to demonstrate foliar water uptake, only 31% of them are from MTC regions and of those found in California, all have been discovered in the last ten years (Emery unpublished). There is a pressing need for understanding the influence of foliar water uptake on the water balance of species in coastal California shrublands, a region that experiences a warmer and drier climate than all other MTCs (Cody and Mooney 1978) and where fire is considered an important structuring force (Keeley and Fotheringham 2001, Franklin et al. 2005).

Previous studies of foliar uptake from around the world have measured water status and gas exchange the morning after a night of fog exposure (Cole 2005, Limm et al. 2009, Eller and Oliveira 2013, Berry and Smith 2014). Yet in many MTC regions overnight fog events are followed by dry, sunny conditions during the day. Additionally, multiple nights of fog inundation may be necessary to alleviate drought stress in MTC species. While the effects of

multiple foggy nights have been explored previously (Simonin et al. 2009), few studies have examined MTC shrub species. This study sought to characterize the accumulation of fog effects on shrub species over several days and whether the influence of overnight foliar wetting lasts through mid-afternoon, when air temperatures peak.

In this study I address the following questions: (1) How do shrub species respond physiologically to overnight foliar wetting, and does this response differ based on foliar morphology and life history traits? (2) Which species demonstrate direct foliar uptake? And (3) How do plant responses change with several consecutive nights of fog exposure? To understand the physiological impacts of overnight fog and presence of foliar uptake, individual potted plants were exposed to artificial fog over the course of four sequential nighttime treatments. During the experiment, midday xylem pressure potential, live fuel moisture and morning photosynthesis were measured for control and treatment plants. To determine if foliar uptake of fog occurred, fog was labeled with deuterium-enriched water and plant samples evaluated for the δD ratio before and after the first night of fog treatment.

METHODS

Study Species

This study investigates how fog and foliar uptake affects the physiology and flammability of five coastal California shrub species. The study species were selected based on several criteria: a widespread distribution along the California coast, likelihood of experiencing fog inundation in wild populations, different leaf habit (evergreen or drought-deciduous), and variation in leaf morphology. Two of the study species are dominants in the local chaparral community, a sclerophyllous shrub-dominated plant community found at mid-elevations in California (Hanes 1977). In the Santa Barbara region, this plant community receives higher annual rainfall than lower elevations and summer fog tends to

occur primarily in May and June (Fischer et al. 2009, Emery unpublished). *Adenostoma fasciculatum* is found throughout California, has small tough needle-like leaves and variable rooting depth (Kummerow et al. 1977). The second chaparral species, *Ceanothus megacarpus*, is found on south-facing slopes of coastal chaparral in southern California. It has small sclerophyllous leaves and tends to have shallow roots (Hellmers et al. 1955, Schlesinger et al. 1982). Both species are considered to be strongly drought tolerant (Jacobsen et al. 2007) and as part of the coastal chaparral ecosystem, experience occasional summer fog (Leipper 1994, Fischer et al. 2009).

The three other shrub species are primarily found in California sage scrub (CSS), a plant community at lower elevations near the coast of central and southern California (Westman 1981), although they can also occur as an early successional plant community within chaparral (Hanes 1971). *Salvia leucophylla* and *Artemisia californica* are drought-deciduous, shallow-rooted shrubs that comprise CSS (Kirkpatrick and Hutchinson 1977). In contrast, *Baccharis pilularis*, is a fast growing, generally deep-rooted shrub with evergreen glabrous leaves (Wright 1928, Ackerly et al. 2002) that commonly occurs within CSS, open grasslands and areas of recent disturbance within chaparral (Kirkpatrick and Hutchinson 1977).

This study sought out genotypes from the Southern California coast, a region that experiences wildfires (Keely and Fotheringham 2001) and summer fog events (Leipper 1994) as foliar water uptake can vary within a species across their geographic range (Limm and Dawson 2010). Individual plants of *Salvia leucophylla* (n=11), *Artemisia californica* (n=12), *Baccharis pilularis* (n=11) and *Ceanothus megacarpus* (n=10) used in the experiment were local genotypes of the Santa Barbara Region purchased in 2011 from Santa Barbara Natives Nursery (Santa Barbara, CA). *Adenostoma fasciculatum* (n=10) individuals

were from the Southern California coast and purchased from El Nativo Growers, Inc (Somis, CA) in 2011. *Adenostoma fasciculatum*, *Baccharis pilularis* and *Ceanothus megacarpus* were repotted to 5 gallon pots with Sunshine® Mix #5 (Sungro). *Salvia leucophylla* and *Artemisia californica* were repotted with 2/3 Sunshine® Mix #5 (Sungro), 1/3 sand as advised by the Santa Barbara Natives Nursery. The plants were kept outdoors on greenhouse benches for over a year prior to the experiment to allow for acclimatization to the local climate. All individuals were potted at the same time and any effects of becoming root bound in the pots are likely to have affected all plants equally. During this acclimatization period, plants were well watered every 1-1.5 weeks to encourage growth of the plant canopy.

Fog chamber construction

To expose shrubs to a controlled fog treatment, a chamber was constructed out of PVC piping and Tyvek sheeting. The box-shaped chamber had an intake and exit hole so that there was sufficient airflow and fog could move through the chamber. The dimensions were 1.25m by 1.25m by 2m. To generate fog, an ultrasonic fog-generating humidifier with an internal fan system was used to direct fog into the chamber (MH10 Industrial Ultrasonic Humidifier, Mainland Mart Corp., El Monte, CA). The machine volatilizes water with vibrating ceramic discs without chemicals or heat (similar to Limm et al. 2009, Berry and Smith 2014). Approximately one liter of water was volatilized per hour and passed through the chamber. To ensure constant supply of water to the machine, a reservoir was constructed to allow water to passively flow into the machine for the duration of the overnight treatments. The flow of water from the reservoir to the machine was controlled by a float valve.

Experimental setup

This study was conducted in the fall of 2013 at the UC Santa Barbara greenhouse facilities on the UC Santa Barbara campus at approximately 30m elevation and within 1km of the coast. Because the size of the fog chamber could only fit one species at a time, each species was tested in sequence. All plant species not undergoing the experiment were housed outside of the greenhouse on benches. The dates of treatment were different for each species in the fall of 2013: 10/13-10/17 *B. pilularis*, 10/20-10/24 *S. leucophylla*, 10/27-10/31 *C. megacarpus*, 11/3-11/7 *A. fasciculatum*, 11/12-11/16 *A. californica*. From October to mid-November in Santa Barbara, outside temperatures ranged from 22°-9°C with an average temperature of 16°C. For the duration of each experiment, all plants being tested were kept inside a climate-controlled greenhouse. Every evening for four nights, experimental plants were placed in the fog chamber and taken out every morning. Control plants were located in the same greenhouse as the treatment plants to experience similar ambient conditions but they stayed in that greenhouse overnight while the treatment plants were in the fog chamber. Temperature, relative humidity and leaf wetness were recorded using Decagon sensors (Decagon Devices, Pullman, Washington) placed inside the fog chamber and in the greenhouse adjacent to the control plants for the duration of the experimental period.

Fog treatment and ambient conditions

The greenhouse ambient conditions mimicked fall weather conditions and were allowed to fluctuate between 15°-27°C from 7:00 to 17:00 and 10°-15° C with 99% RH (or approaching 99%) from 17:00 to 7:00 the next morning. Fog treatments consisted of the fog machine running from 0:00 to 6:00 each day. This period of time is typically when Santa Barbara experiences nighttime fog (personal observations, Fischer et al. 2009). Maintaining constant fog inside the chamber was difficult after sunrise so the treatments were ended just prior to sunrise at 6:00. There were four consecutive nights of fog treatment with the first

night consisting of isotopically labeled water followed by three nights of unlabeled water supplied by the greenhouse. For the first night of fog, greenhouse water was labeled with D_2O in order to increase the δD ratio to 100 per mil above the background greenhouse water level used in fog treatments. To prevent contamination, control plants were moved to a nearby greenhouse with the same controlled conditions only for the first night of fog treatment. Labeled fog was only used for one night for each species to reduce isotopic contamination of the water vapor in the greenhouse. For the subsequent three nights of fog treatment, water from the greenhouse was used and the control plants were kept in the same greenhouse as the fog chamber.

Plant preparation

After purchase and repotting in 2011, shrubs were well watered for over a year prior to the experiment. Exactly 14 days prior to the beginning of the experimental period for each species, individual plants were given a single watering of 600ml. This study attempted to mimic summer drought conditions by withholding water from potted shrubs for two weeks prior to experimental treatment. Pre-treatment TDR (Time-Domain Reflectrometry) of soil water for all species averaged 4.6% ±2.5 (SD) soil water content. In order to prevent fog water absorption by roots, the soil surface was isolated from fog drip. During the afternoon prior to the experimental period, pots were placed in an autoclave bag and wrapped to the base of the plant stem. A 2'x2' square piece of polyurethane tarp was placed on top of the bag at the base of the plant and sealed to the base with waterproof adhesive tape and Smartbond® Landscape Construction Adhesive (DAP Products Inc). The tarp was draped over the pot and secured to it with cord. This process closed off the base of the plant to prevent water entering the soil without permanently sealing the pot off from air. The overnight bagging and securing procedure was performed on both control and treatment

plants for each night of the experiment. Every morning the tarp was untied and autoclave bag removed, exposing the soil surface to the surrounding atmosphere. During daylight hours, the tarps remained on top of the pots for both control and treatment plants as the seal at the base of the stem was permanently fixed.

Measurements

Soil Moisture

To determine if water from the treatment leaked into the soil, soil moisture was measured using a 10cm MiniTrase TDR soil moisture probe (Model #: 6050X2, SoilMoisture Inc, Goleta, California). Measurements were taken the night before (18:00), the first morning after treatment (8:00) and the morning after the 4th night of treatment (8:00). To take a measurement, the tarp was lifted slightly to allow the TDR probes to enter the top 10cm of soil at the base of the stem. Two measurements on opposite sides of the main stem were averaged to produce a measurement for soil moisture. While relative error in TDR measurements increases when soil water content is low (Skierucha 2000), a 10cm probe is still accurate for measuring absolute soil water content (Noborio 2001). Soil water isotope samples were also collected before and after the first night of fog treatment and were scheduled for analysis if there was a difference in soil moisture. Based on soil moisture results from the TDR probe, soil water isotope samples were not analyzed.

Xylem Pressure Potential and Live Fuel Moisture

Xylem pressure potential (XPP) was measured with a Scholander-type pressure chamber (Model 1000, PMS Instrument Comp., Corvallis, OR). To measure XPP, a terminal segment of suberized stem with several leaves was clipped, sealed in a plastic bag and placed in a dark cooler until measurements could be made in the laboratory. Less than 30 minutes elapsed between clipping stems and measurements on the pressure chamber. Midday (15:00-

16:30) XPP measurements were taken the day prior, day 1 and day 5 of the experiment. Individual plants were designated treatment or control based on their pre-treatment xylem pressure potential. The lowest XPP was designated as a control, second lowest as treatment and alternated henceforth. This was done to prevent accidental bias of initial plant condition. For some species, the control and treatment groups differed in sample size by one individual. The sample sizes for all species and treatments were constrained by the size of the fog chamber. XPP was measured at midday to reduce measurement error from leaf wetness, to observe potential lagged effects of nighttime foliar wetting, and to coincide with live fuel moisture measurements. Immediately before measuring XPP, each stem sample was weighed ("Wet Weight"). After measuring XPP in the laboratory, the sample was placed in a drying oven at 80^0C for 48 hours to obtain the "Dry Weight." Live fuel moisture (LFM) was calculated according to the United States Forest Service as

$$LFM = \frac{Wet\ Weight - Dry\ Weight}{Dry\ Weight}$$ (Countryman and Dean 1979). After clipping of any plant tissue on the potted plant, the plant stem was sealed with a thermosetting adhesive to prevent water uptake through cut stems during subsequent nights of fog treatment.

Photosynthesis

Photosynthesis, stomatal conductance and transpiration were measured with a LI-6400 (LI-COR, Lincoln, Nebraska) the morning (9:00-10:00) before fog treatments began and the morning (9:00-10:00) after the 4th night of fog exposure. Fog exposure ended at 6:00 and the chamber was opened between 7:00-8:00. The 9:00 timing was sufficiently long enough to allow for water on leaves to be absorbed or evaporate from the overnight fog treatment. Two groups of leaves per plant (1-3 leaves depending on the species) were measured with

the LI-6400 and then removed to quantify leaf area. This study used ImageJ software (NIH, USA, http://rsb.info.nih.gov/ij/) to calculate leaf area and adjust the LI-6400 measurements.

Stable Isotopes

Leaves and suberized stem tissue adjacent to selected leaves were sampled the evening before (18:00) the first night of fog using procedures from Limm et al. (2009). This method consists of spraying leaf tissue with DI water and patting dry before collecting and freezing tissue for later analysis. This same sampling procedure was conducted approximately an hour after the first fog treatment ended (7:00) to wash off any labeled water from the surface. Plant samples were separated into leaves and stems, sealed in scintillation vials with Parafilm and placed in a -10*C freezer. To determine the δD ratio for each sample, water was extracted at the Center for Stable Isotope Biogeochemistry, University of California Berkeley using cryogenic vacuum extraction (Ehleringer et al. 2000) and analyzed with an Isotope Ratio Mass Spectrometer (model Delta plus XL; Finnigan MAT, Breman, Germany).

Analysis

To test for and remove outliers, the Dixon test was performed for each set of data and species (Dixon 1950). For each analysis, the Brown-Forsythe test for equal variance (Brown and Forsythe 1974) was used for control and treatment plants for each species. For the measurements with equal variance a Student's t-test was performed and subsequently a sequential bonferroni to correct for multiple tests across the five species. If the variance was unequal, the Alexander Govern test (Alexander and Govern 1994) was used and p-values corrected using a sequential bonferroni. All p-values reported are corrected family-wide p-values at the 0.05 alpha level. All analyses were conducted using JMP Pro 11 (SAS Institute, Cary, North Carolina). Plant species could not directly be compared because they were tested on separate dates.

Leaf surface images

Leaves from all five species were selected for surface imaging to examine foliar surface morphology. Environmental scanning electron microscopy (ESEM) was performed in the Micro-Environmental Imaging and Analysis Facility at the University of California at Santa Barbara (https://www.bren.ucsb.edu/facilities/MEIAF/) under NSF Awards BES-9977772 and DBI-0216480. Images were taken in May, 2015 and April, 2016. Leaves were destructively sampled from the plants used in this study (Fig 1).

RESULTS

Environmental conditions and soil moisture

The environmental sensors indicated that greenhouse conditions (where the control plants resided) were broadly similar to the fog chamber in both temperature and relative humidity (Fig 2). During the period of fog exposure, temperatures were 6^0C higher inside the fog chamber. This is likely due to the ultrasonic volatilization process heating up the fog water. Relative humidity was also higher due to the presence of fog throughout the experimental chamber.

The leaf wetness sensor detected higher condensation inside the fog chamber compared to the surrounding greenhouse (Fig 2), indicating fog saturation in the overnight treatment. Treatment plants generally had wet leaves until 8:00-9:00 the morning after fog exposure as can be observed with the leaf wetness sensor (Fig 2). Between 8:00-9:00 is when the chamber was opened and treatment plants placed in the open area of the greenhouse.

For soil moisture, there was no significant difference between treatment and control individuals for any of the five shrub species after one night or four nights of fog treatment (Table 1). Average soil moisture across all species increased slightly for treatment individuals from 4.22% ±0.9 (SD) to 4.31% ±1.1 (SD). Average soil moisture across all

species decreased slightly for control individuals from 4.39% ±0.9 (SD) to 4.24% ±0.9 (SD). The non-significant differences in soil moisture between treatment and control individuals for all species indicate that roots and soil were effectively isolated from fog water during overnight treatments.

Plant water isotopes

The δD ratio for the leaves of treatment plants was significantly enriched compared to the control (Fig 3) for *A. fasciculatum* (p=0.0028), *A. californica* (p=0.0005), *B. pilularis* (p=0.0039),) and *S. leucophylla* (p=0.007). Only *C. megacarpus* showed no significant enrichment compared to the control (p=0.3318).

The δD ratio for stems of treatment plants was significantly enriched compared to the control (Fig 3) for two of the species: *B. pilularis* (p=0.003) and *S. leucophylla* (p=0.023). There was no significant difference between control and treatment for *C. megacarpus* (p=0.4459). While *A. fasciculatum* (p=0.4459) and *A. californica* (p=0.2149) were also not significantly different, treatment plant average was slightly enriched by 8.37 and 6.8 δD per mil respectively compared to the control plant average.

Live fuel moisture

A single night of fog treatment had little effect on live fuel moisture for treatment plants across all species (Table 2). While there was no significant difference in LFM change between control and treatment after four nights of fog treatment, treatment plants of all species tended to have increased LFM compared to the controls (Table 2). The average difference between treatment and control across all species was a 14% (SE ±4.8%) increase in LFM for plants exposed to overnight fog treatments.

Xylem pressure potential

After one night of fog, midday XPP was marginally higher in the treatment plants for *A. fasciculatum* (p=0.09, Table 3). *C. megacarpus, B. pilularis, S. leucophylla* and *A. californica* showed no significant difference in XPP after one night of fog treatment. After four nights of fog exposure, four of the five shrub species showed no significant difference in midday XPP between control and treatment (Table 3). *Salvia leucophylla* was the only species with significantly higher XPP in treatment plants compared to control individuals (p=0.0445).

Photosynthesis & stomatal conductance

For the evergreen species, *C. megacarpus, A. fasciculatum* and *B. pilularis*, both treatment and control individuals experienced a decrease in photosynthetic rates during the experimental period, likely due to lack of watering (Table 4). The two drought-deciduous shrubs, *A. californica* and *S. leucophylla*, maintained photosynthetic rates under the fog treatment with *S. leucophylla* treatment plants having marginally higher rates than control plants (p=0.0885). Photosynthetically active radiation was maintained at 1800 µmol mol^{-1}. Across all species, leaf temperature averaged 26.09^{0}C ± 0.12 (SE) and vapor pressure deficit derived from leaf surface temperature averaged 2.25 kPa ± 0.02 (SE). There was improved stomatal conductance for *A. fasciculatum* treatment plants compared to the control (p=0.043, Table 5). *A. californica, B. pilularis* and *S. leucophylla* tended to have improved stomatal conductance after four nights of fog compared to the controls. Ci/Ca was also evaluated and no significant trends or differences were found for all species.

DISCUSSION

Species differences in foliar water uptake

Four of the five shrub species demonstrated foliar water uptake based on the δD isotopic ratios (Fig 3). The only species without an isotopic signal of fog in leaf or stem tissue was *C.*

megacarpus. While the leaves of this species are small and sclerophyllous, these foliar characteristics are also shared by *A. fasciculatum* and *B. pilularis*. *C. megacarpus* is a member of the subgenus *Cerastes* which is known to have stomatal crypts (Nobs 1963). This recessed stomatal anatomy is thought to reduce transpiration (Turner 1994) and enhance gas exchange (Hassiotou et. al. 2009). It is possible that stomatal crypts in *C. megacarpus* reduce contact between stomates and condensed water droplets on the leaves thus making it difficult for plants to take up water. Stomatal uptake of water has been observed previously (Burkhardt et al. 2012) and foliar water uptake capacity decreases with increased leaf hydrophobicity (Lekson et al. 2015). In addition to stomatal crypts, *C. megacarpus* has trichomes (Fig 1) which may increase hydrophobicity and the distance between water droplet and leaf interior. While stomatal crypts and trichomes may have affected FWU for *C. megacarpus*, the general mechanism of FWU is still under debate (Qiu et al. 2010).

Evidence suggests that foliar water can enter through the cuticle (Yates and Hutley 1995, Kersteins 1996, Eller et al. 2013), leaf epidermal hydathodes (Martin and von Willert 2000) and stomata (Burgess and Dawson 2004, Burkhardt et al. 2012). The four shrub species in this experiment that demonstrated foliar water uptake have very different leaf morphologies, phenologies and stomatal control. Although *A. fasciculatum* and *B. pilularis* are both evergreen, *A. fasciculatum* has small sclerophyllous needle-like leaves while *B. pilularis* has glabrous leaves with a relatively thick cuticle. In contrast, the drought-deciduous species *A. californica* and *S. leucophylla* have "softer" leaves that curl and turn brown during the summer, weak stomatal control, and high transpiration rates compared to evergreen chaparral species (Harrison et al. 1971). A notable anatomical difference is the shape of their leaves; *S. leucophylla* has broad elliptical leaves while *A. californica* has feather-like leaves with a high surface area to volume ratio. Atmospheric water may enter through thin cuticles

or through the stomata in these species. Both *A. californica* and *S. leucophylla* have a dense layer of trichomes that cover both sides of a leaf (Fig 1). These structures may enhance FWU as trichomes in other species have been shown to facilitate water uptake in leaves (Benzing and Burt 1970, Martin and von Willert 2000). Additionally, circadian rhythms of stomatal conductance (Resco de Dios et al. 2013) may affect the relative uptake of water through stomata during different times of day or night. Foliar water uptake occurred in four plant species in this study, despite large differences in leaf morphology, suggesting that there may be multiple mechanisms operating simultaneously to facilitate foliar water uptake in these Mediterranean type shrub species.

In two of the shrub species, *S. leucophylla* and *B. pilularis*, isotopically enriched water was also evident in stem tissue (Fig 3). Previous isotopic research has focused on detecting foliar water uptake in leaf tissue alone (Limm et al. 2009, Berry and Smith 2014). Evidence for water transport in xylem through foliar absorption has been detected with reversal of sap flow in several tree species that experience regular fog inundation (Burgess and Dawson 2004, Eller et al. 2013). Alternatively, the enriched water may have been taken up through bark. Recent work has demonstrated bark water uptake in Coastal redwoods (*Sequoia sempervirens*; Earles et al. 2015). For *S. leucophylla* and *B. pilularis* fog water present in stem tissue indicates reversal of sap flow and/or bark water uptake. Either mechanism suggests that these two species can benefit from foliar uptake of fog water.

Plant Water Content

Although all five shrub species periodically experience fire disturbance, they are distributed across different fire regimes along the California coast. An important correlate of fire size in the shrub-dominated ecosystems of coastal California is live fuel moisture (Dennison and Moritz 2009), which is likewise a key component of plant flammability

(Anderson 1970, Martin et al. 1994). For all five shrub species in the Santa Barbara region, LFM tends to decrease during the summer drought until the first fall rains occur (LACFD 2015, Emery unpublished). Summer fog may affect plant water relations for these species as there is evidence of fog water use for *A. californica* in late summer (Emery and Lesage 2015). From the evidence presented by this study, FWU alone appears to slightly increase LFM after several nights of fog exposure (Table 2). Due to the short timescale of this study, the slight increase is likely due to water uptake and not from changes in dry matter content (Jolly et al. 2014). It is possible that FWU might contribute to water conservation, reducing loss of plant water content during the summer months. Coastal fog influence on plant flammability is likely dependent on the quantity of fog present and the ability for shrubs to take up fog water through surface roots, a means of water uptake that was excluded in this study.

Previous work on FWU has shown that taking up water through leaves improves water status (Gouvra and Grammatikopoulos 2003, Breshears et al. 2008, Limm et al. 2009, Berry and Smith 2014). In this study, fog effects on midday XPP were minimal except for *S. leucophylla* (Table 3). This species has high transpiration rates under drought conditions (Harrison et al. 1971) suggesting the possibility of stomatal water uptake. FWU in *S. leucophylla* may improve hydraulic functioning and reduce tension in xylem tissue. For the remaining three species that demonstrated FWU, it is possible that any difference in plant water status between control and treatment is lost by midday. While foliar wetting of *A. californica* leaves increases pre-dawn XPP (Cole 2005), this study found no difference between control and treatment plants for *A. californica* (Table 3). Treatment plants for all five species tended to have higher stomatal conductance in the morning (Table 5), meaning more transpiration and water loss. This could result in similar XPP for control and treatment

plants by midday. This is particularly relevant to Mediterranean-type climate regions which can experience overnight fog events followed by hot, dry weather the following afternoon. The results of this study suggest that FWU has temporary benefits to plant physiology, and the improvements may not be easily detected by the afternoon following fog immersion.

It is also possible that the experimental conditions inhibited the improvement of overall water status as measured by XPP. Drought conditions stimulate abscisic acid accumulation, limiting stomatal response in many plant species (Zhang et. al. 2006). Initial XPP measurements indicate that all species had relatively low water potentials prior to the experimental period (Table 3). Despite exposure to fog for several nights, foliar uptake may have been inhibited by biochemically mediated limitations in stomatal response. For *Sequoia sempervirens,* well-watered leaves absorbed more fog water than water-stressed leaves (Burgess and Dawson 2004). Although conditions were meant to reflect a summer drought typical of the Santa Barbara region, low levels of leaf hydration in this experiment could have reduced the effects FWU on plant water status.

Photosynthesis

Foliar water uptake of fog may supplement water availability in leaves, enhancing morning photosynthesis during the dry summer months. Treatment individuals for the two drought-deciduous species had increased photosynthetic rates and the species with FWU tended to have improved rates compared to the controls (Table 4). Compared with chaparral species, *A. californica* and *S. leucophylla* have rapid physiological responses to rain events (Gray 1982, Cole 2005). These two species may be more responsive to foliar wetting during summer droughts, allowing for more summertime CO_2 assimilation. Additional carbon resources during drought could then enhance hydraulic function by providing resources for repair and maintenance (McDowell 2011). This summertime carbon gain may also prolong

leaf lifespan for drought-deciduous species that likely drop leaves due to water availability (Harrison et al. 1971). Despite an overall reduction in photosynthetic rates over the course of the experiment for evergreen species (*B. pilularis*, *C. megacarpus* and *A. fasciculatum*), the treatment plants for the two species with FWU (*B. pilularis* and *A. fasciculatum*) tended to have higher photosynthetic rates with fog exposure than controls (Table 4). Overnight wetting of leaves for *A. fasciculatum* and *B. pilularis* may provide a small boost in photosynthesis during the early morning hours of the day. The results of this study suggest that FWU can maintain photosynthetic activity in drought-deciduous species and buffer the loss of CO_2 assimilation in evergreen species with thicker, more sclerophyllous leaves.

Conclusions

Fog influences on plant water relations are well established in regions with consistent, high quantities of fog deposition such as montane cloud forests (Scholl et al. 2011, Goldsmith et al. 2013, Eller et al. 2013, Gotsch et al. 2014), the redwood forests of Northern California (Burgess and Dawson 2004) and bishop pines on the Channel Islands (Fischer et al. 2009, Baguskas et al. 2016). Much less is known about semi-arid ecosystems with highly variable fog deposition such as the shrublands of coastal California. While fog can be variable across years (Williams 2009), it can provide significant moisture during the summer drought (Hiatt et al. 2012, Vasey et al. 2012). This study found that for many species, overnight foliar wetting of leaves can result in water uptake. In the species with foliar water uptake, fog treatment plants tended to have higher stomatal conductance and photosynthetic rates. Few plants reacted to a single night of fog treatment suggesting that several consecutive nights of fog exposure may be necessary to significantly affect shrub physiology.

California shrublands, like many Mediterranean-type climates, experience seasonal drought and periodic wildfires. While coastal fog in California provides shading and water for several woody species (Burgess and Dawson 2004, Fischer et al. 2009, Vasey et al. 2012, Carbone et al. 2013, Baguskas et al. 2016), fog patterns may be changing (Johnstone and Dawson 2010, Williams et al. 2015). For plant communities in arid regions, foliar absorption of atmospheric water may provide a critical supplement during periods of drought. From this study, it appears that drought-deciduous species (*A. californica* and *S. leucophylla*) benefit more from overnight fog events than evergreen species (*A. fasciculatum, B. pilularis* and *C. megacarpus*). This differential response to fog exposure in California shrub species may affect how plant communities and ecological interactions change under future climate scenarios.

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TABLES AND FIGURES

Table 1. Mean soil moisture (% water content ±SE)

Species	Initial	Change after one night		Change after four nights	
		Control	Treatment	Control	Treatment
A. californica	3.74 ± 0.34	0.19 ± 0.08	0.21 ± 0.04	-0.1 ± 0.10	0.43 ± 0.42
A. fasciculatum	3.57 ± 0.17	-0.36 ± 0.15	-0.35 ± 0.14	-0.74 ± 0.31	-0.4 ± 0.12
B. pilularis	4.87 ± 0.16	0.29 ± 0.08	0.56 ± 0.27	0.13 ± 0.19	0 ± 0.10
C. megacarpus	4.71 ± 0.10	0.02 ± 0.05	-0.15 ± 0.11	-0.45 ± 0.14	-0.27 ± 0.12
S. leucophylla	4.58 ± 0.17	-0.19 ± 0.12	0.4 ± 0.28	0.03 ± 0.17	0.6 ± 0.33

Table 2. Mean live fuel moisture (% ± SE). Change is post-exposure minus pre-exposure.

Species	Initial	Change after one night		Change after four nights	
		Control	Treatment	Control	Treatment
A. californica	69.87 ± 2.84	2.79 ± 4.79	12.89 ± 13.60	0.29 ± 6.14	11.18 ± 8.04
A. fasciculatum	91.48 ± 5.72	-0.33 ± 3.53	5.35 ± 3.52	-9.27 ± 5.55	0.73 ± 5.89
B. pilularis	100.09 ± 10.90	-4.05 ± 9.58	0.37 ± 8.47	-29.22 ± 17.82	3.36 ± 9.32
C. megacarpus	69.65 ± 3.47	-4.94 ± 1.35	-2.82 ± 0.98	-6.03 ± 1.26	-6.71 ± 1.46
S. leucophylla	67.71 ± 3.09	3.24 ± 3.64	8.58 ± 6.42	-0.87 ± 1.81	12.76 ± 6.54

Table 3. Mean xylem pressure potential (MPa ± SE). Change in midday xylem pressure potential is post-exposure minus pre-exposure). * α = 0.05 significance threshold.

Species	Initial	Change after one night		Change after four nights	
		Control	Treatment	Control	Treatment
A. californica	-3.22 ± 0.27	0.03 ± 0.03	-0.03 ± 0.08	0.79 ± 0.20	0.46 ± 0.33
A. fasciculatum	-4.36 ± 0.54	-0.11 ± 0.08	0.31 ± 0.10	0.35 ± 0.26	-0.08 ± 0.08
B. pilularis	-3.57 ± 0.27	-0.09 ± 0.09	-0.08 ± 0.09	-0.15 ± 0.60	0.46 ± 0.34
C. megacarpus	-6.26 ± 0.18	-0.28 ± 0.12	-0.15 ± 0.10	-0.48 ± 0.20	-0.33 ± 0.13
S. leucophylla	-6.32 ± 0.27	-0.01 ± 0.10	0.33 ± 0.17	-0.16 ± 0.10	1.80 ± 0.70*

* α = 0.05 significance threshold

Table 4. Mean photosynthetic rate (µmol CO2 m^{-2} s^{-1} ± SE). Change in photosynthetic rate is post-exposure minus pre-exposure.

Species	Initial	Change after four nights	
		Control	Treatment
A. californica	12.54 ± 1.54	-1.45 ± 2.13	1.16 ± 2.12
A. fasciculatum	9.72 ± 1.26	-5.57 ± 1.24	-3.46 ± 1.26
B. pilularis	9.75 ± 1.80	-7.51 ± 2.09	-3.62 ± 0.75
C. megacarpus	6.49 ± 1.02	-2.69 ± 1.30	-4.83 ± 0.73
S. leucophylla	5.42 ± 1.18	-3.72 ± 1.10	1.33 ± 1.29

Table 5. Mean stomatal conductance (mmol m^{-2} s^{-1} ± SE) Change in stomatal conductance is post-exposure minus pre-exposure. * α = 0.05 significance threshold.

Species	Initial	Change after four nights	
		Control	Treatment
A. californica	136.8 ± 11.6	-40.82 ± 16.32	14.01 ± 35.13
A. fasciculatum	103.8 ± 11.6	-98.36 ± 5.65	-59.14 ± 8.51*
B. pilularis	42.5 ± 8.3	-32.72 ± 6.94	-15.38 ± 6.20
C. megacarpus	30.1 ± 5.2	3.58 ± 7.28	10.60 ± 8.26
S. leucophylla	61.0 ± 11.3	-14.74 ± 14.34	15.73 ± 11.26

* α = 0.05 significance threshold

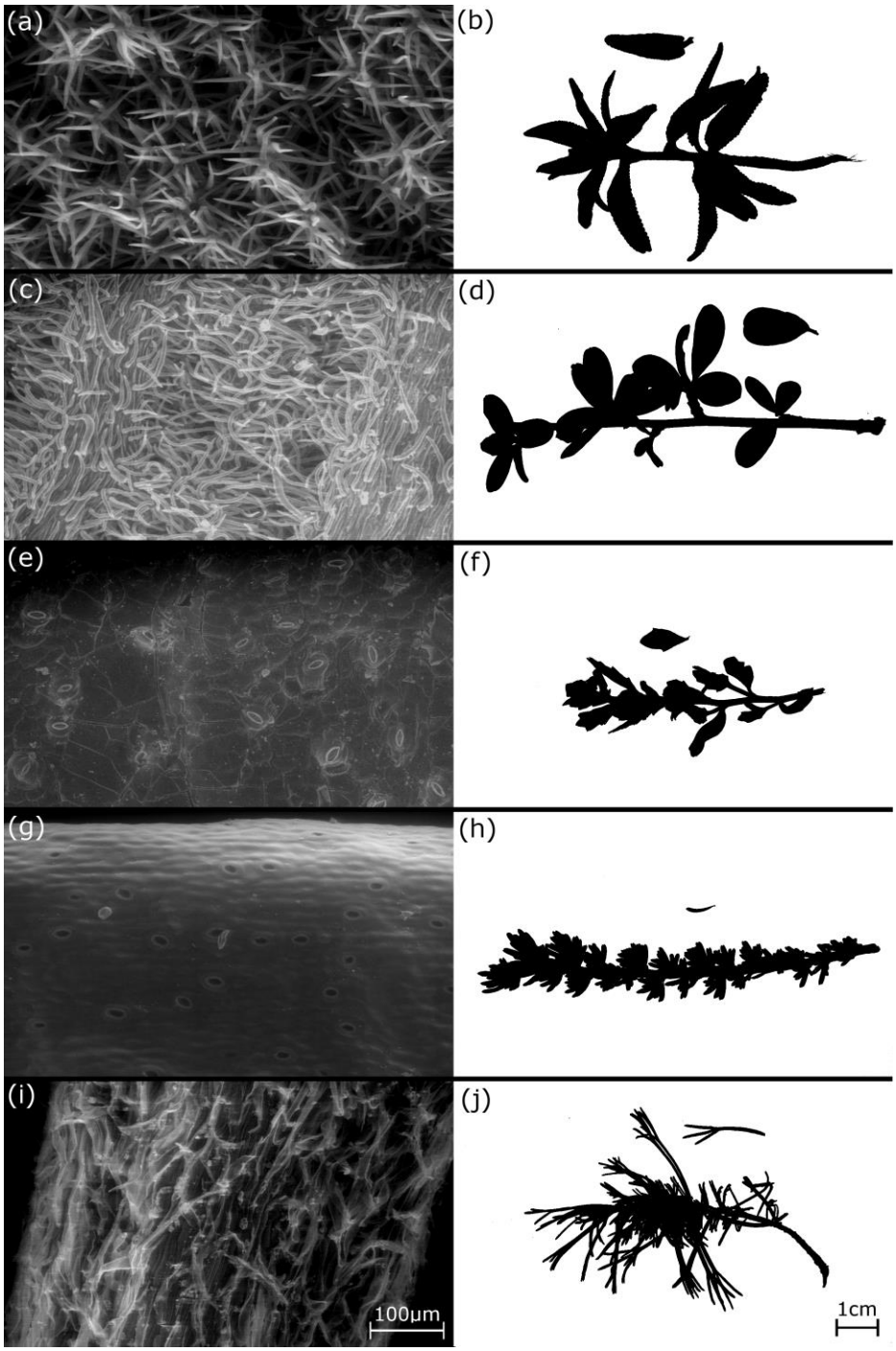

Figure 1. Environmental Scanning Electron Microscope images and corresponding silhouettes of branches with a single leaf for the adaxial side of *S. leucophylla* (a, b), the abaxial side of *C. megacarpus* (c, d), the adaxial side of *B. pilullaris* (e, f), the adaxial side of *A. fasciculatum* (g, h), and the adaxial side of *A. californica* (i, j).

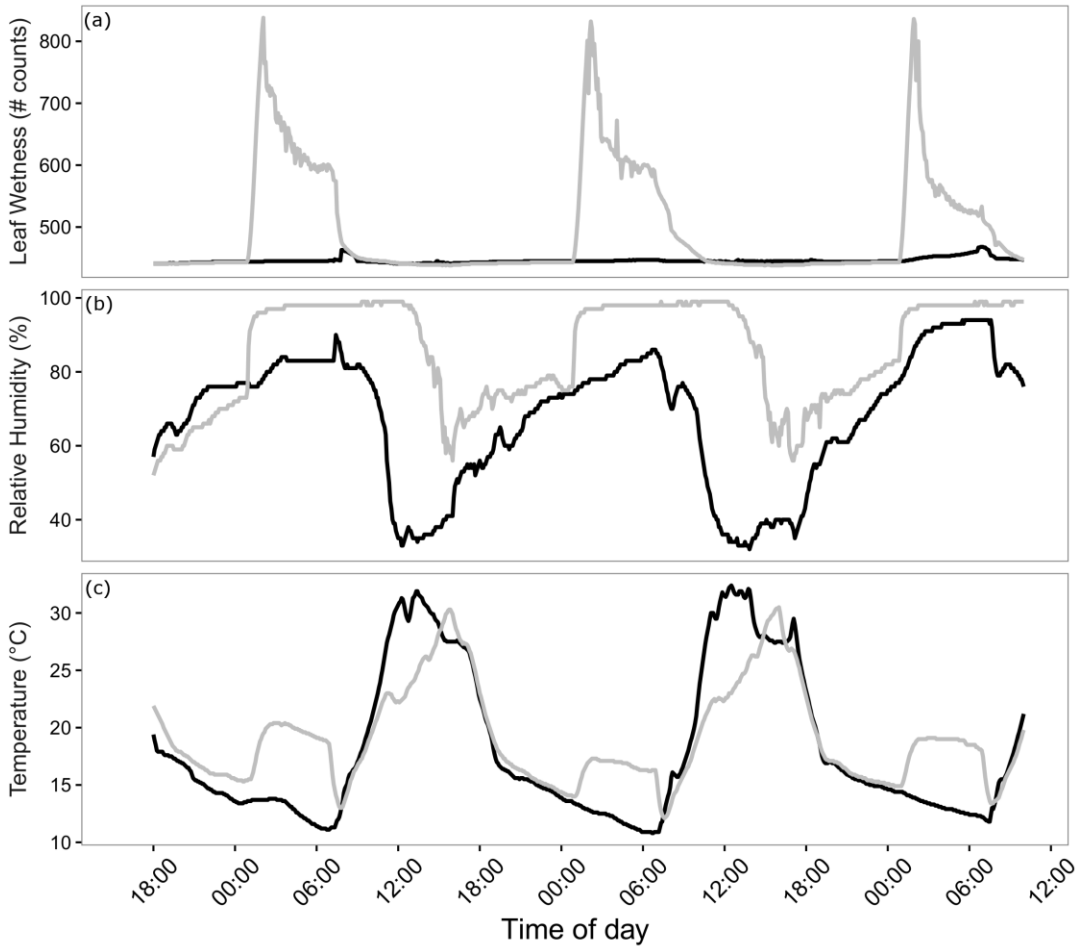

Figure 2. Representative leaf wetness (a), relative humidity (b), and temperature (c) data for three nights of fog treatment (0:00-6:00) from 28-Oct-2013 to 31-Oct-2013. Control is in black, fog treatment is in gray.

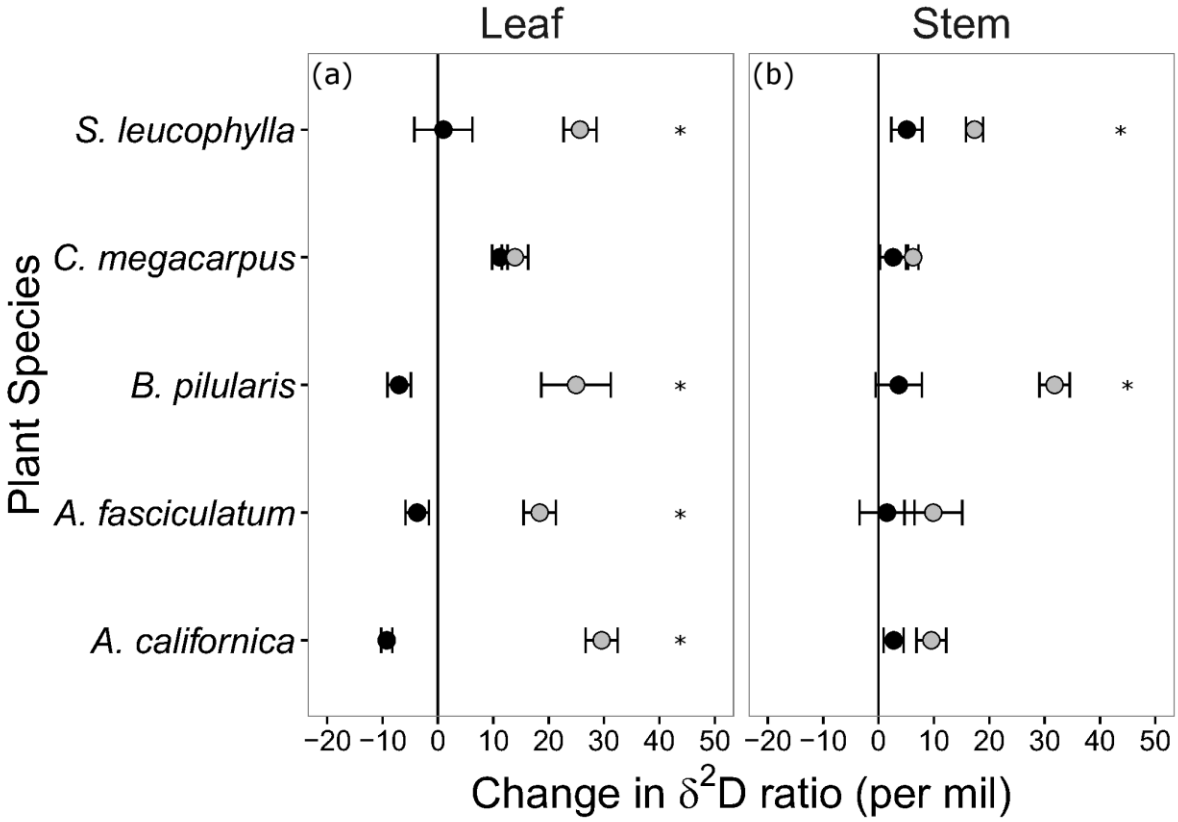

Figure 3. Change in the δD ratio after one night of fog treatment for leaves (a) and stems (b) for post-exposure minus pre-exposure. Control plants are in black, fog treatment plants in gray. Points are the mean value with standard error bars. * α = 0.05 significance threshold.

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Chapter III: Fog and Live Fuel Moisture in Coastal California Shrublands

ABSTRACT

As research on fog has increased, so has our understanding of how fog influences ecosystems, yet many unknowns remain. In many Mediterranean-type climates, seasonal drought causes plants to dry out which facilitates wildfire disturbances. Along the California coast, summer fog has the potential to ameliorate drought conditions and reduce plant flammability. This study investigated how dry season fog affects live fuel moisture in six dominant shrub species from chaparral and sage scrub plant associations. Fog water uptake was evaluated using stable isotopes of hydrogen and oxygen at several field sites in Santa Barbara County. In order to determine the effects of fog on live fuel moisture across the dry, summer months, multiple environmental measurements and indices including fog deposition were combined into principal components and these scores were regressed against the live fuel moisture loss rate across the summer drought. While fog water uptake was identified in all five shrub species tested for isotopic composition, it was highly variable among individuals within a population. We further found that fog water was a significant correlate of live fuel moisture loss rate in the two drought-deciduous shrub species, but not in any of the evergreen species. It is likely that fog water uptake fluctuates based on localized fog deposition which in turn is affected by topography, the elevation in which vegetation intercepts clouds and plant position within a stand. In coastal California, fog is an important water source, and although used opportunistically, it can reduce live fuel moisture loss rates for some species during the summer drought.

INTRODUCTION

Ecological research on plant water relations often investigates how plants acquire water and the relative importance of different sources of water for ecosystem function (Phillip

1966, Dawson et al. 1993, Asbjornsen et al. 2011). These fundamental questions have led to the exploration of the importance of clouds as a direct water source in ecosystems around the world. While clouds have indirect effects on plants such as reducing solar insolation thereby reducing evapotranspiration (Williams et al. 2008, Fischer et al. 2009, Carbone et al. 2013, Baguskas et al. 2014), direct cloud water use in the form of fog uptake can improve water balance (Limm et al. 2009, Emery 2016), enhance carbon assimilation (Berry and Smith 2013, Gotsch et al. 2014) and increase hydraulic function (Laur and Hacke 2014). Fog can also affect community and ecosystem-level processes by changing hydrological cycling through the input of water (Dawson 1998, Matimati 2009, Scholl et al. 2010, Sawaske and Freyburg 2015), thereby altering demography (Baguskas et al. 2016) and affecting range distributions of species (Limm and Dawson 2010). These effects may be pronounced in seasonally dry ecosystems such as the Mediterranean-type climate region of coastal California.

In four of the five Mediterranean regions, including California, wildfire is a natural part of the disturbance regime. While these natural fire regimes are influenced by many factors, in southern California extreme fire weather (Davis and Michaelsen 1995, Moritz et al. 2010) and live fuel moisture (Dennison et al. 2008, Dennison and Moritz 2009) are important drivers of wildfire patterns. Live fuel moisture, the ratio of water to dry material in live plants (LFM; Countryman and Dean 1979), is a critical component of plant flammability (Anderson 1970, Martin et al. 1994), indicative of fire intensity (Green 1981) and is incorporated into many fire danger rating systems (Weise et al. 1998, Chuvieco et al. 2004). During the summer drought, LFM generally declines (Miller and Poole 1979) and this pattern of decline is strongly influenced by spring precipitation (Dennison and Moritz 2009). During the summer drought, significant fog events occur along the California coast (Leipper

1994, Rastogi et al. 2016). These provide shading and moisture for plants (Williams et al. 2008, Fischer et al. 2009, Baguskas et al. 2014, Emery and Lesage 2015), potentially altering patterns of LFM decline, yet this has not been previously investigated.

While fog could contribute to patterns of LFM, other climatic variables such as rainfall, temperature, relative humidity, wind and solar insolation may also influence the rate of decline in LFM over the summer months. Previous research on the predictors of LFM has investigated seasonal rainfall, drought and fire weather condition indices such as the Keetch-Byram Drought Index (KBDI; Keetch and Byram 1968), Canadian Fire Weather Index (CFWI; Van Wagner 1987) or Fosberg Fire Weather Index (FFWI; Fosberg 1978). The Keetch-Byram Drought Index has been shown to predict LFM of shallow-rooted herbaceous species but not deep-rooted trees (Dimitrakopoulos and Bemmerzouk 2003). The Drought Code, a component of the CFWI, has been used to predict LFM of shrubs in the Iberian Peninsula (DC; Viegas et al. 2001) and Italy (Pellizzaro et al. 2007). The Fosberg Fire Weather Index combines weather conditions which can influence plant water content (Anderson 1982) and has been used in efforts to model fuel moisture content (Sharples et al. 2009). While these indices incorporate climatic data in various forms, they lack information on fog inundation. During periods of no rain, LFM loss may change depending on fog, cloud immersion, and the ability of plants to take up fog water.

For much of coastal California, fog frequency (Leipper 1994, Fischer et al. 2009, Rhastogi et al. 2016) and fire disturbance patterns (Keeley and Fotheringham 2001) differ by elevation. Chaparral is a sclerophyllous shrub-dominated plant association that tends to grow at mid to high elevations (Hanes 1977). While fire frequency for this association is highly variable, the natural fire return interval for southern California chaparral is considered to be 30-80 years depending on the location (Franklin et al. 2001, Keeley and Fotheringham 2001,

Moritz et al. 2009). At lower and typically drier elevations, sage scrub is the dominant plant association and it is characterized by several drought-deciduous species (Westman 1981) and less frequent fire disturbance (Keeley et al. 2005). While previous studies have demonstrated that several species within these systems have the potential to take up fog (Cole 2005, Emery and Lesage 2015, Emery 2016), there have been no investigations of how summer fog affects LFM patterns.

This study investigates fog water uptake in coastal Mediterranean California shrub species during the annual summer drought and how fog deposition and climate influence LFM in species from two different plant associations. It specifically addresses the following questions:

1. Do coastal California shrub species use fog water during the summer drought and how does this differ between species from chaparral versus sage scrub associations?
2. How does fog deposition affect LFM trends of these species relative to climatic indices and other meteorological factors during the summer drought period?

Fog frequency along the California coast is inherently variable (Leipper 1994, Lewis et al. 2003), thus fog water use can be difficult to detect and will be influenced by the quantity of fog deposition. When fog encounters plants, the water adheres to vegetation, drips to the soil surface and wets the upper layers of soil (Fischer and Still 2007, Carbone et al. 2011). We hypothesize that sage shrub species at lower elevations were more likely to encounter low-lying clouds and take up fog through shallow roots or through foliar uptake (Emery 2016). LFM for all species is likely to be influenced by multiple environmental factors, however, lower elevation species are more likely to experience fog events as fog is typically more

common below 400m in this region (Fischer et al. 2009). Thus we predict that summer fog is more likely to reduce LFM loss in the sage scrub association compared to chaparral.

METHODS

Site selection

This study was conducted at four field sites in Santa Barbara County, CA. The greater region experiences a Mediterranean-type climate with hot, dry summers and cool, wet winters. The four sites include two along the coast and two in the more interior Santa Ynez Valley. The Santa Ynez Valley lies north of the two coastal sites and the E-W running Santa Ynez Mountains. The field sites were chosen to represent locations of low and high fog frequency, respectively. The sites were selected based on vegetation association, accessibility and proximity to a meteorological station. The two plant associations are chaparral and sage scrub with one site of each vegetation type in each of the coastal and valley areas. Chaparral tends to grow at higher elevations than sage scrub, receives more rainfall, and is dominated by evergreen sclerophyllous shrubs (Hanes 1977). Sage scrub grows at lower elevations and is largely comprised of drought-deciduous shrub species (Westman 1981).

The coastal field site for sage scrub was at El Capitan State Beach (34°28’N, 120°01’W) in summer of 2011 and Coal Oil Point Reserve for 2012-2013. The shift was due to restrictions placed on sampling at El Capitan State Beach. El Capitan State Beach will be referred to as Sage Scrub Coastal One (SSC1, see Figure 1) and is located 16.5 km west of the University of California Santa Barbara. The vegetation there consists of *Baccharis pilularis, Artemisia californica* and *Salvia leucophylla*. The soil type is Milpitas-Positas fine sandy loam (El Capitan General Plan, 1979). Coal Oil Point Reserve, (SSC2, Figure 1), is part of the University of California Natural Reserve System and is located two km west of

the University of California Santa Barbara campus (34 24'N, 119 52'W). The climate at Coal Oil Point Reserve is very similar to El Capitan State Beach with a mean precipitation of 441±8 mm per year and mean temperatures of 6^0C in January and 24^0C in August (UCNRS 2014). At Coal Oil Point Reserve there are stands of *Artemisia californica* and *Baccharis piluaris*, but not *Salvia leucophylla*. The soil is Concepcion fine sandy loam with intrusions of clay. The chaparral coastal field site (CHC, Figure 1) was located on private property along Painted Cave Road at 800 meters in elevation above the city of Santa Barbara, CA (34 30'N, -119 47'W). According to the nearby San Marcos weather station located 3 km west of CHC at the same elevation, mean January temperature is 12^0C, mean August temperature is 22^0C and mean annual rainfall is 868±472mm. The chaparral association at this field site is a mesic chaparral association with a mix of *Adenostoma fasciculatum, Ceanothus megacarpus*, other *Ceanothus* species, and *Arctostaphylos* species. The soil is derived from Coldwater sandstone parent material (Dibblee 1966).

The sage scrub interior field site (SSI, Figure 1) is located in Sedgwick Reserve, part of the University of California Natural Reserve System, 7.3 km northeast of Los Olivos, CA (34 41'N, 120 2'W) 24 km from the coast. The field site is at 425m elevation with a mean January temperature of 10.5^0C, mean August temperature of 19^0C, and mean annual rainfall of 561 mm. SSI is an uplifted Pleistocene alluvial terrace and is mapped as consisting of Ballard Series soils that are generally fine sandy loams or gravelly fine sandy loams (Shipman, 1972). The fog collector and weather station are located adjacent to a mixed stand of *Artemisia californica* and *Salvia leucophylla* (Roberts et al. 2010). Nearby lies a stand of *Baccharis pilularis*, located 0.5 km to the southwest of the weather station and considered part of the SSI field site. The chaparral interior field site (CHI, Figure 1) was located in Sedgwick reserve 4.8 km north of SSI along Figueroa Mountain Road and consisted of

mixed *Adenostoma fasciculatum* and *Ceanothus cuneatus*. The soil type is a Toomes-Climara complex. The field site is at 730m elevation and according to the Figueroa Mountain RAWS weather station (991m elevation, 1.9km east of CHI), mean January temperature is 12^0C, mean August temperature is 26^0C and mean annual rainfall is 544±253mm.

Species selection

We chose to evaluate dominant species in the sage scrub association with different phenologies and rooting depths. *Artemisia californica* is a drought-deciduous shrub considered to have a shallow root system (Kirkpatrick and Hutchinson 1977) and it has been shown to use fog water in the late summer (Emery and Lesage 2015). By contrast, *Baccharis pilularis* is a deep-rooted evergreen shrub found throughout California (Wright 1928, Ackerly et al. 2002) but it too is abundant in the coastal zone. *Salvia leucophylla* is a drought-deciduous species with broader leaves than *A. californica* and a patchier distribution (Kirkpatrick and Hutchinson 1977). Little is known about its rooting depths. *Artemisia californica* and *B. pilularis* were measured from 2011-2013 while *S. leucophylla* was measured only for the 2011 field season, as SSC2 lacked *S. leucophylla*.

Chaparral is typified by evergreen sclerophyllous-leaved shrub species (Hanes 1977). *Adenostoma fasciculatum* is a widespread evergreen shrub and has small needle-like leaves (Kummerow et al. 1977). This species can have variable rooting depth (Kummerow et al. 1977) and is the main species measured by the US Forest Service to monitor fire danger in chaparral (Burgan 1979). This study focused on two species of the genus *Ceanothus*, *C. megacarpus* for the coastal field site and *C. cuneatus* for the interior field site. Both species are in the subgenus *Cerastes*, a more drought-tolerant subgenus of *Ceanthous* (Davis et al. 1999). Of all *Ceanothus* species, *C. megacarpus* and *C. cuneatus* tend to occupy areas of

high drought severity (Meentemeyer and Moody 2002) and are resistant to water stress-induced cavitation (Davis et al. 1999). *Ceanothus megacarpus*, in particular, is a highly drought tolerant evergreen shrub species (Gill and Mahall 1986, Jacobsen et al. 2007).

Water isotopes and tracking of fog uptake

This study used stable isotopes of hydrogen and oxygen to track fog water uptake into stem tissue (Dawson et al. 2002). Isotopic analyses were conducted at each field site except for CHI as no fog deposition was detected there. At each of the other field sites (SSC1, SSC2, SSI and CHC), groundwater, rainwater and fog water were collected for three years (2011-2013) and analyzed for their stable isotopic ratio. Groundwater was collected from man-made wells within one kilometer of each field site. Rainwater for the SSC1 and SSC2 field sites was collected at SSC2 (Coal Oil Point Reserve). Rainwater was also collected at CHC and SSI and brought to the lab after every rain event. A Nalgene container with several centimeters of mineral oil was used to prevent evaporative fractionation and trap rainwater for isotopic analysis. For all field sites except for SSC1, fog deposition was measured using a fog collector modified from Fischer et al. (2007) containing a Nalgene with several centimeters of mineral oil. The container was swapped out approximately every two weeks in the field and brought to the lab to measure volume, extract the water and filter using a 0.45 µm cellulose acetate filter. Fog collectors were not permitted at SSC1, so fog water data from SSC2 was used for SSC1. Fog, rain and groundwater samples were analyzed for stable isotopes of hydrogen and oxygen using Isotope Ratio Infrared Spectroscopy at the Stable Isotope Biogeochemistry Lab at UC Berkeley. Fog and rainwater collection occurred at SSC2, CHC and SSI for all three years of the study. Fog collection only occurred during the summer months, from May to the first rainfall of the fall. Rain water isotopic values were used to develop a local meteoric water line for the Santa Barbara region.

In semi-arid environments, water isotopes in the upper soil profiles experience evaporative fractionation. As a result, the isotopic ratio of water taken up by roots is generally more enriched in the heavier isotope than the source water isotopic ratio. Using the method outlined by Corbin et al. (2005), we developed evaporative correction regressions for sage scrub and chaparral plant associations. This consisted of taking soil water isotope samples from the soil surface (0-2 cm) and from 2-5 cm depth at one hour intervals from sunrise to midday. Sampling across this time interval captures evaporative fractionation of soil water isotopes and represents how fog or rainwater may fractionate upon entering the soil surface. Four soil sampling events at SSC2 (4/26/2013, 7/10/2013, 8/26/2013, 4/5/2014) and two at CHC (6/7/2013, 8/12/2013) were taken over the summers of 2013 and 2014 to develop regression lines for the two plant associations. The slopes of both depths were similar within sites so the data were aggregated by site to develop evaporative corrections. These association-specific regression lines were used to correct plant water samples for all field sites to the local meteoric water line (see supplementary material, Appendix I). The SSC2 correction was used for sage scrub sites SSC1, SSC2 and SSI. The CHC correction was used for the chaparral site CHC. In order to propagate error associated with the evaporative corrections, we included the 95% confidence interval of the slope for each regression along with the mean slope when running the mixing model for plant water samples.

To develop a reference soil oxygen isotope profile, soil water samples were collected at two locations within the CHC and SSC2 field sites on 7/5/2012 and 9/12/2012. At midday, five soil samples were collected at 0-5 cm, 5-10 cm, 10-20 cm and 30-50 cm in depth. The soil was placed in a 20ml scintillation vial, the lid sealed with parafilm and immediately frozen for future extraction (see supplementary material, Appendix I). Soil water isotopes can vary widely across sampling locations and time of year (Gazis and Feng 2004). The profile

developed for this study is not meant to be an extensive record, but act as a reference for interpretation of isotope ratios at these field sites.

Plant stem water samples were collected monthly in 2011 and twice monthly in 2012 and 2013 in order to ensure capture of samples from before and after measureable fog events. Sampling consisted of clipping 10cm of suberized stem from an individual shrub, quickly removing the bark, placing in a 20ml scintillation vial, placing parafilm over the lid and immediately freezing for future extraction. Stem samples were collected from three individuals per species per site on each date of LFM collection for three years.

Fog detection in stem water

To evaluate whether all species and individuals could use fog, the authors reviewed the fog deposition record at a given field site and selected stem samples that had been taken prior to and after a significant period of fog deposition. To contain costs, only one date following the largest deposition of fog was selected for isotopic analysis for each field site. As no measureable fog was collected at CHI, no stem samples were analyzed for this site. Preference was given to late summer fog events when spring rainfall was less likely to influence the water budget of a given shrub individual (see Table 1). All stem and soil samples were extracted using cryogenic vacuum extraction (Ehleringer et al. 2000) in laboratory of Dr. Christopher Still at UC Santa Barbara and the Stable Isotope Biogeochemistry Lab at UC Berkeley. The stem and soil water samples were then analyzed for hydrogen and oxygen isotopes on an Isotope Ratio Mass Spectrometer (model Delta plus XL; Finnigan MAT, Breman, Germany) at the Stable Isotope Biogeochemistry Lab at UC Berkeley.

We used the SIAR (Stable Isotope Analysis in R) package in R (Parnell et. al. 2010) to determine proportional fog water uptake in all five shrub species. The Bayesian mixing

model incorporates uncertainty associated with the isotopic ratios of water sources and estimates the proportional use of a given water source. Stem water isotopes were generally more enriched than source isotopes (Figures 2-4) and needed to be corrected for evaporative fractionation. When entering the stem water isotopic ratio into the model, we included the 95% confidence interval of the slope associated with the corrected stem water samples. Each individual plant sample was represented by 3 isotopic ratios, the mean corrected value and the two 95% confidence intervals. This is a conservative approach to determining the proportion of fog water in stem tissue, as it incorporates error and uncertainty associated with correcting for evaporative fractionation in arid soils. We used the Markov chain Monte Carlo (MCMC) method with a Dirichlet distribution ("siarmcmcdirichletv4") for each field site. The Trophic Enrichment Factor (TEF) and concentration dependence were set to 0 and the model was for 500,000 iterations with the first 50,000 discarded. All statistical analyses were accomplished using R version 3.3.0 (R Core Development Team, 2016).

Live fuel moisture sampling

The standard US Forest Service procedure for sampling LFM involves collecting plant material at 2:00 PM on dry days, with a max stem diameter of 1/8thin and removing dead material and reproductive tissue. It also includes the separation of plant material into new and old LFM (Countryman and Dean 1979). For certain species in this study, particularly *B. pilularis*, it was impractical to remove all reproductive tissue and for others it was difficult to consistently differentiate between old and new plant material. In order to compare LFM across all six species in a repeatable way, a method was developed for LFM sampling that integrated new and old plant material present at any given time point. In the field, two south-facing (when possible) live branches were randomly selected and 15 cm of terminal stem were removed and placed in a water-tight Nalgene container. A small sample

was taken to reduce the physiological impact of LFM sampling on the same individual over a summer season. No more than 30% of the sample was reproductive tissue and all material along the 15 cm was included except for visibly dead material, which was removed. Due to travel limitations among field sites, sampling was not simultaneous and occurred between 1:00 PM and 5:00 PM on fog-free days. Once collected, samples were brought back to the lab at the University of California Santa Barbara. They were wet weighed, oven dried at 80^0C for at least 48 hours and reweighed. LFM was calculated as:

$$LFM = \frac{Wet\ weight\ (g) - Dry\ weight\ (g)}{Dry\ weight\ (g)}$$

LFM measurements began after what was anticipated to be the last spring rainfall and ended with the first large rain event of the fall season. For the 2011 field season, LFM was measured once a month for 12 individual plants per species per site. Measurements began in April and continued until November 2011. For 2012 and 2013, LFM was measured twice a month for 10 individuals per species per site. Measurements for 2012 began in July and went until September, while in 2013, sampling started in May and went until September. Because this study used a different LFM sampling method than that of the US Forest Service, the authors compared the two methods for *A. fasciculatum*. This species, a chaparral dominant, is the most commonly measured species in Californian USFS inventories. In June, July and August of 2014 we measured ten individual shrubs at the CHC field site using our method, as well as the USFS method of separating new LFM and old LFM (Countryman and Dean 1979). The LFM values obtained by our method are very similar to the average of old and new LFM (see supplementary material, Appendix II). A linear regression between the average of new and old LFM (USFS) and the method used in this study yields a linear relationship with a slope of 0.91 and an R^2 of 0.92. This suggests that our method accurately

reflects the LFM of *A. fasciculatum* across the season. It thus appears to be appropriate for comparing LFM across multiple California shrub species, particularly when it is difficult to separate old and new plant material.

Predicting LFM using meteorological factors and indices

This study used meteorological data from nearby weather stations to quantify climatic conditions and several drought and fire behavior indices for analysis of LFM data. Meteorological data was collected from weather stations at SSC2 (used for SSC1 and SSC2), CHC and SSI (Roberts et al. 2010). For 2011 until June of 2012, meteorological data for CHC came from the San Marcos Pass weather station (ID: KCASANTA45), 2.5km west of CHC at 600m in elevation. After June of 2012, meteorological data was measured at the CHC field site. Environmental conditions at CHI were taken from the nearby Figueroa Mountain RAWS weather station (991m elevation, 1.9km east of CHI). Meteorological data used in the analysis included mean temperature, relative humidity, rainfall, vapor pressure deficit and dew point depression (Summarized information is available in supplementary materials Appendix V). For the central California coast, a study found that fog deposition was positively correlated with dew point depression (Hiatt et al. 2012). In addition to meteorological data, this study also quantified fog deposition using fog collectors modified from Fischer et al. (2007) with Nalgene containers to collect fog water. Fog water was collected during the summer months approximately every two weeks. It was difficult to determine when fog deposition occurred during a sampling period so the volume of fog water collected was divided by the number of days elapsed between two sampling dates. This metric, fog per day, represents the average daily fog deposition during the summer drought.

All environmental factors and indices were aggregated over the two weeks prior to a given LFM sampling date for statistical analyses (see supplementary material, Appendix V). Two weeks was the minimal LFM sampling interval and as daily environmental conditions are unlikely to affect LFM, it was important to aggregate over a period of time preceding a LFM measurement.

We used R version 3.3.0 for all analyses (R Development Core Team 2014). Because many of the aggregated indices and environmental factors were correlated, we used the princomp() function from the stats package in R to perform a principal components analysis (PCA) of the potential factors. All variables were log-transformed to control for different scales prior to undergoing PCA. As many sites as possible were included in the PCA in order to accurately account for covariance among environmental correlates. For the field sites CHC, SSC1, SSC2 and SSI, three principal components (PCs) explained 80.2% of the variance. PC 1 was composed of primarily vapor pressure deficit, relative humidity, the Duff Moisture Code and the Build-Up Index. PC 2 was composed of mainly the Drought Code and Fosberg Fire Weather Index. PC 3 is mostly derived from fog deposition. For the CHI field site, which did not have fog deposition for the duration of the study or solar insolation data available, a separate PCA was necessary yielding three principal components that explain 91.9% of the variance. PC 1 was composed primarily of vapor pressure deficit, dewpoint depression and temperature. PC 2 was mainly composed of the Fosberg Fire Weather Index and wind. PC 3 was derived from the Drought Code and relative humidity. The PCs differed slightly between analyses and the loadings can be found in supplementary material (Appendix III and IV). These principal components were used to understand the environmental controls of LFM loss during the summer drought.

Live fuel moisture analysis

This study explored environmental factors that affect the change in LFM over a time interval because a single LFM measurement does not reflect the direction of moisture loss or gain. An individual shrub may have decreasing or increasing LFM when a measurement is taken. The direction of LFM change should be directly related to antecedent climatic conditions. During the summer months, LFM tends to decrease along an exponential decay function (Figure 5). In order to understand the change in LFM from one date to the next, we modeled the proportional rate of change in LFM from time point 1 to time point 2. The resulting LFM rate was the following:

$$\text{LFM Loss Rate} = \log\left(\frac{LFM_{timepoint1}}{LFM_{timepoint2}}\right)/(Number\ of\ days\ elapsed)$$

Environmental Influences on LFM: Linear Mixed Effects Model

We chose to use a linear mixed effects model to determine the relative influence of environmental factors, drought and fire weather indices, and fog deposition on the summertime rate of LFM loss for each shrub species. LFM loss rate was analyzed by species, including all field sites where those species were found. This means, for example, that *C. cuneatus* was only evaluated at CHI, while *B. pilularis* was evaluated at SSC1, SSC2 and SSI. All years of LFM data were used in the analysis. For each individual plant, the initial LFM at the start of each summer was designated a fixed effect as the LFM loss during the summer is affected by how well hydrated the plants are at the beginning of the summer. Additionally, "shrub individual" was designated as a random effect as individual shrubs at the same field site tended to follow a similar pattern of LFM change across each summer season.

For each species, the three principal components were run for the linear mixed effects model using the maximum likelihood method from the nlme package in R. Using

Akaike's Information Criterion (AIC), models of LFM loss rate were ranked (Table 2). When the model for PC3 had the lowest AIC, except for *C. cuneatus*, the significance of fog was evaluated separately using the linear mixed effects and the restricted maximum likelihood approach to determine significance of fog on the LFM loss rate for a particular species.

RESULTS

Fog Collection

Fog deposition across years was highly variable and differed among field sites (Figure 6). In 2011 there was fog at both CHC and SSC2 in the early summer (May/June) as well as in the late summer at SSC2 (August/September). For all three years at the interior field site, SSI, fog deposition was low throughout the summer months and the water collected likely included dew deposition. No fog water was collected at CHI for all three summers of the study. Reviewing the fog collection record enabled efficient selection of stem samples to run for water isotope analysis (Table 1). Samples were selected from before and after a significant fog event at each field site.

Water sources and their isotopic signatures

As expected, fog water was more enriched in the heavier isotopes of hydrogen and oxygen compared to groundwater and rain for the three sites that experienced fog deposition, sage scrub coastal, chaparral coastal, and sage scrub interior (Figures 2-4). The isotopic ratio of fog water was similar between the two coastal sites (CHC, SSC2) and slightly depleted in the hydrogen isotope for the interior site (SSI). At the sage scrub coastal sites, rain was variable and slightly enriched compared to groundwater for both sites (SSC1 and SSC2, Figure 2). At the chaparral coastal site (CHC, Figure 3) and sage scrub interior site (SSI, Figure 4), rain was slightly more depleted than groundwater. The local meteoric water line

(LMWL), y = 7.5684x + 8.0852, was developed from three years of rainwater isotopes from all field sites. Plant water samples for all species were more enriched in the hydrogen and oxygen isotopes than the water sources and fell to the right of the LMWL (Figures 2-4).

For both CHC and SSC2, the oxygen isotopic ratio was depleted for the top layer of soil (see supplementary material, Appendix I). Subsequent depths were initially more enriched near the top layer and became more depleted with depth. These patterns are typical of arid, low rainfall climates (Hsieh et al. 1998). For all soil depths the oxygen isotopic ratio was more enriched in the heavier isotope for SSC2 than for CHC.

The regression for soil water evaporation fractionation differed by field site (see supplementary material, Appendix I). Consistent with the soil oxygen isotopic profile, soil water was generally more enriched at SSC2 compared to CHC. The slope of the regression at CHC was 2.76 and 3.33 at SSC2.

Fog water uptake

The SIAR mixing model reveals that all five species of shrubs exposed to fog used some fog water in the intervals over which their tissues were collected (Figure 7). The proportions were highly variable and differed slightly by species and shrub individual (identified by shape in Figure 7). For each field site, there are individual shrubs that appear to increase in fog proportion after the fog event, while other individuals do not change or even decrease in fog proportion. Surprisingly, little difference was detected among species for a given field site. The lack of species-specific differences may be explained by the uncertainty of the true plant water isotopic ratio after accounting for evaporative fractionation.

Live fuel moisture analysis

The patterns of LFM loss during the summer drought period followed an exponential decay function (Figure 5). Most study species lost water rapidly in the early summer and approached an asymptote by mid-summer. Of all the species measured, *B. pilularis* maintained relatively high LFM throughout the late summer months.

The principal components were composed of multiple aggregated environmental factors and indices (see loadings in Appendix III and IV). The principal component analysis for CHC, SSC1, SSC2 and SSI yielded three PC's that explained 80.2% of the variance. PC1 was primarily driven by VPD, RH, the Duff Moisture Code, and the Build-Up Index. These represent atmospheric moisture and modeled litter moisture content. PC2 was primarily composed of the Drought Code and the Fosberg Fire Weather Index, and models shallow soil moisture and fire weather conditions. PC3 was primarily driven by fog deposition. For the CHI field site, which had no fog deposition or solar insolation data, a separate PCA explained 91.9% of the variance. PC1 was driven by RH, Dewpoint Depression, Temperature and the Canadian Fire Weather Index. PC2 was driven primarily by the Fosberg Fire Weather Index and Wind. PC3 was composed mainly by the Drought Code and RH. The results of the linear mixed-effects model selection differed by plant association and life history (Table 2). In chaparral, the best model for predicting the LFM loss rate in *A. fasciculatum* was PC2 representing shallow soil moisture and fire weather conditions. The LFM loss rate of *C. megacarpus* was best predicted by PC1 representing atmospheric moisture and litter water content. In neither case did PC3 (fog) play a role. At the CHI field site, PC3 (which did not include fog), or shallow soil moisture, best explained LFM loss rate in *C. cuneatus*.

In the sage scrub association, the LFM loss rate of the two drought-deciduous species was best predicted by PC3 which represents fog deposition. *Artemisia californica* and *Salvia*

leucophylla were also influenced by fog alone using the linear mixed effects model with a restricted maximum likelihood method (*A. californica*, $p=0.014$; *S. leucophylla*, $p<0.0001$). The LFM loss rate for *B. piluaris*, on the other hand, was best predicted by PC1 representing atmospheric moisture and litter water content.

DISCUSSION

Despite high variation in fog deposition across sites and years, some plants in the chaparral and sage scrub associations take up fog water during the summer drought. While all species exposed to fog show isotopic evidence of fog water uptake, there was high variation among individuals before and after fog events (Figure 6). Despite variable proportions of fog water in plant tissue, summer fog appears to slow the rate of LFM loss for the two drought-deciduous species (Table 2). The influences on LFM loss rate for the four evergreen shrub species differed by species and depended on drought conditions as well as weather. Both fog water uptake and changes to LFM in shrubs are likely dependent on micro-site differences, and the frequency and quantity of fog deposition.

Fog patterns and plant water uptake

Fog deposition was highly variable among field sites and years (Figure 6). Fog tends to occur along the coast in the early summer at both low (SSC2) and high elevations (CHC). However, late summer fog primarily occurred at lower elevations. Fog deposition at the nearby Channel Islands reflects a similar pattern with summer clouds remaining below 400m in elevation (Fischer et al. 2009). This suggests that chaparral species at higher elevations do not experience late summer fog as frequently and are thus less likely to be influenced by this water source during the summer drought. These the patterns of cloud-base height along the California coast may change in the future as cloud levels rise from urbanization (Williams et al. 2015) or changing climatic patterns. Urban development at lower elevations may reduce

fog inundation for the sage scrub association if nighttime warming occurs from the urban heat island effect (Oke 1982). In the Santa Ynez Valley, at SSI, fog deposition was low but consistent throughout the summer (Figure 6). This could reflect early morning dew that registers as fog, however, early morning fog is known to occur in the Santa Ynez river basin (Upson and Thomasson 1951). Fog deposition patterns, while variable, may change in the future particularly if upwelling patterns change as increased upwelling increases the marine cloud layer along the California coast (Bakun 1990, Snyder et al. 2003).

Although fog water uptake was detected in the five shrub species sampled, the proportion of fog water was highly variable among individuals (Figure 6). The quantity of fog condensation and fog drip likely depends on the micro-site location for a given shrub individual. Personal observation from an unpublished study on fog chemistry at SSC2 supports the observation that fog is mostly likely to collect on plants and drip to the soil along the windward edge of a stand. This directional pattern of deposition has been observed in Chilean forests with windward edges receiving significantly more fog than the leeward edge (Del-Val et al. 2006). Hence, the position of a shrub within the landscape at a very local scale could influence the amount of fog water intercepted and taken up by the individual.

Variable fog frequency during the summer drought suggests that fog water uptake is an opportunistic event for many plants and is not frequent enough or in high enough quantity to influence all shrub individuals for a given plant association. Fog water uptake can be highly variable among species as observed in northern Californian plant associations (Dawson 1998, Corbin et al. 2005). In chaparral, *A. fasciculatum* and *C. megacarpus* can use fog water during the summer months (Figure 7). However, the proportion of fog water was low and did not significantly increase after the one fog event where we measured it. Prior to

sampling, there was a rain event which may have provided rain water to belowground roots (Table 2) and kept the proportion of fog water to rain water constant during the sampling period. Fog drip usually wets the litter layer and top few centimeters of soil (Ingraham and Matthews 1995, Dawson 1998, Corbin et al. 2005, Fischer and Still 2007, Carbone et al. 2013). If chaparral shrubs have roots primarily distributed at greater depths, they are unlikely to access fog drip. *A. fasciculatum* is reported to have a variable rooting system while *Ceanothus* species tend to have relatively shallow roots (Hellmers et al. 1955, Kummerow et al. 1977, Kummerow et al. 1978). Most shrub canopies in the chaparral study area are very tall (>2 meter), and cover the entire soil with two meters of stems and leaves. We observed that fog events during the study rarely penetrated the canopy to the ground beneath these dense canopies. Yet the isotopic evidence suggests fog water is taken up by these species so it is likely that this fog water is taken up through foliar uptake. In a greenhouse study using labeled water, Emery (2016) did find evidence that *A. fasciulatum* could take up fog through the foliage, but did not find evidence of foliar uptake in the co-occurring species *C. megacarpus*.

In the sage scrub association, all three study species can undergo foliar uptake of fog (Emery 2016) and all showed fog water uptake during the late summer months here (Figure 7). These results are consistent with previous work showing fog water use in *A. californica* during the late summer (Cole 2005, Emery and Lesage 2015). The two drought-deciduous species, *A. californica* and *S. leucophylla* appear to readily use fog deposition in the field and can have upwards of 30% of their water come from fog (Figure 7). These two species have shallow roots (Kirkpatrick and Hutchinson 1977) and are known to use small rain events (Gray 1982). The drought-deciduous shallow-rooted strategy likely enables these species to tolerate summer drought and respond to small precipitation events, including fog

events. Late summer fog may also spur new growth in *A. californica* prior to the first fall rain events (Emery, *personal observations*). While *B. pilularis* can use fog water through foliar uptake (Emery 2016), root uptake is also possible. At all three field sites, *B. piluaris* was using a non-trivial proportion of fog water, even when compared to *A. californica* (Figure 7). While *B. piluaris* is thought to have deep roots that tap into groundwater (Wright 1928, Ackerly et al. 2002), established stands can still have roots present in the top 15cm of soil (Zavaleta and Kettley 2006) and potentially access fog drip in the summer months. Fog water may be important for young *B. pilularis* to establish (Kidder, A. *personal communications*) and act as a supplementary water source as the plants' rooting distribution becomes deeper with age (Zavaleta and Kettley 2006).

Fog and live fuel moisture

Chaparral is a widespread fire-prone association in California (Epling and Lewis 1942, Hanes 1971). In order to understand how fire spreads through ecosystems and fire risk, it is important to measure plant flammability (Anderson 1970, Gill and Zylstra 2005) and LFM is a critical component of plant flammability (Anderson 1970, Martin et al. 1994). Although the chaparral shrub species in this study took up fog early on in the summer drought, fog did not affect the rate of LFM loss at that time. Instead, results from our analyses suggest that shallow soil moisture (DC) and fire weather conditions (FFWI) are important contributors to LFM decline for *A. fasciculatum*, arguably the dominant species across much of coastal California chaparral (Table 2). Previous research has shown that March-May rainfall is critical to the summer LFM decline in *A. fasciculatum* (Dennison and Moritz 2009). These rain events are typically the last precipitation inputs before the summer drought and influence soil moisture over the entire summer drought. In a study in Portugal and Spain, LFM of Mediterranean shrub species was also found to be predicted by the

Drought Code (DC), a model of soil moisture with a 52-day time lag (Viegas et al. 2001). The Fosberg fire weather index (FFWI) models weather and not fuels in an attempt to measure changes in fire weather conditions (Fosberg 1978). Increased fire weather conditions aggregated over a two-week period (the sampling period of this study) may affect plant physiology by increasing evapotranspiration and water loss. *Adenostoma fasciculatum* maintains relatively high water potentials (Poole and Miller 1975) and continues gas exchange (Redtfeldt and Davis 1996) through the summer drought (unpublished data 2nd author). D'Antonio et al. (unpublished) have evidence for a slight increase in photosynthesis by this species after a heavy summer fog event at CHC. But hot, dry and windy conditions should increase foliar water loss and decrease LFM for this species.

For *C. megacarpus*, the LFM loss rate was best predicted by PC1, which represents atmospheric moisture and shallow soil moisture (Table 2). *Ceanothus* species can have shallow rooting systems (Hellmers et al. 1955) and the model results may reflect *C. megacarpus* responding to changes in moisture in the upper layers of soil as the drought ensues. Yet shallow roots might also allow *C. megacarpus* to access fog water (Figure 7). This species remains physiologically active during part of the summer drought (Gill and Mahall 1986) and transpiration may be influenced by VPD. For *C. cuneatus,* LFM loss rate was best predicted by PC3 representing shallow soil moisture and atmospheric moisture. Similar to *C. megacarpus*, *C. cuneatus* may be responding to lack of water in the top 10 centimeters of soil (modeled in the Drought Code). Although no fog was measured at the CHI field site, *C. cuneatus* grows during the summer drought (Baker et al. 1982) and may benefit from fog drip when available.

While there is a LFM threshold for *A. fasciculatum* and fire size in southern California (Dennison and Moritz 2009), LFM of chaparral species may not be as influential

to fire behavior as dead fuels. Retention of dead branches increases fire intensity (Schwilk 2003) and could affect fire patterns in southern California. Additionally, differences in LFM may be more reflective of changes in dry mass and structure instead of water content (Qi et al. 2014). For the chaparral association in the Santa Barbara region, fog was not as frequent during the late summer (Figure 6), possibly explaining why PC3 (fog) did not predict LFM loss rate. In California coastal regions north of Santa Barbara, fog is more frequent (Lewis et al. 2003) and has been shown to increase soil moisture within a chaparral community (Vasey et al. 2012). Given that chaparral species can take up fog water (Figure 7), with more consistent fog in greater quantities it is possible that fog could affect chaparral LFM loss rates in some years.

Fog effects on LFM were more evident in the sage scrub plant association which occurs at lower elevations. LFM loss rate for the two drought deciduous species, *A. californica* and *S. leucophylla*, was best predicted by PC3 representing fog deposition (Table 2). Fog can reduce evapotranspiration (Fischer et al. 2009), lower growth rates with reduced insolation (Williams et al. 2008), and provide a source of water for shrubs in the summer months (Emery and Lesage 2015). All of these effects can positively influence LFM and reduce the dry down rate. These two shallow-rooted shrubs rely heavily on summer water availability to maintain photosynthesis and reduce leaf loss (Poole and Miller 1975). Condensation and dew may also influence water content in sage scrub species as these can be important water resources in arid ecosystems (Agam and Berliner 2006). While this study was unable to measure dew formation, cloud-derived water was important for LFM of the two drought deciduous species.

The LFM of *B. pilularis* stays relatively high during the summer drought (Figure 5). Mature *B. pilularis* tend to have deep roots (Wright 1928, Ackerly et al. 2002, Zavaleta and

Kettley 2006) and may be accessing deeper water sources than the two drought-deciduous species. Although LFM loss rate in *B. pilularis* was best predicted by PC1, representing atmospheric moisture and shallow soil moisture, all PCs were similar in their predictive ability (Table 2). It is possible that climatic factors including fog have little effect on the LFM loss rate as this species tends to maintain high LFM during the summer drought (Figure 5). In the sage scrub association, this evergreen species had proportions of fog uptake comparable to the co-occurring *A. californica* and *S. leucophylla*. This suggests that summer water availability likely influences LFM for all sage scrub species to an extent. While the sage scrub fire regime is little understood, it is possible that summer fog could reduce plant flammability for this low elevation plant association. This is important as the sage scrub association tends to occur where the majority of human habitation lies (Davis et al 1994). Humans are the primary cause of ignitions in southern California and are increasing fire frequency in shrubland ecosystems (Syphard et al. 2007). Thus although ignitions are likely to be high because of human contact with this association, the sage scrub species may sustain less successful ignition and lower fire spread rates because of fog influence on fuel condition.

Conclusion

This study has shown that not only is summer fog taken up by coastal shrub species, but more importantly that it reduces the rate of water loss over the summer months for some species and thus potentially influences their flammability. This influence could become very strong when and if fog inundation is frequent and in high quantity. Although the summer seasons of this study were not particularly foggy compared to fog deposition reported elsewhere in California (Sawaske and Freyburg 2015, Clemesha et al. 2016), fog did slow LFM loss rates for two sage scrub species. This buffering effect on LFM during the fire

season may alter wildfire spread rates across coastal plant associations. By contrast, LFM of higher elevation shrub species that comprise chaparral, were not affected by fog deposition. However, these plant communities did not experience high fog inundation during the late summer, when LFM was lowest. In more northern California coastal shrublands (both sage scrub and chaparral), fog is more consistent and could have an impact on LFM. For many Mediterranean-type climate regions, fog can occur frequently during the dry season thus current models of fire danger and LFM in such habitats should include fog deposition.

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TABLES AND FIGURES

Table 1. Dates selected for stem water isotopic analysis. Plant samples were selected prior to and after a significant fog event at each field site (except for CHI).

Field Site	Species	Date of sampling		Fog collection (ml)	Date of last rainfall (>6mm)
		Pre-fog	Post-fog		
CHC	*A. fasciculatum, C. megacarpus*	5/3/2013	5/17/2013	245.7	5/6/2013
SSC1	*A. californica, B. pilularis, S. leucophylla*	8/30/2011	9/29/2011	217.2	6/6/2011
SSC2	*A. californica, B. pilularis*	8/12/2013	9/3/2013	94.5	4/1/2013
SSI	*A. californica, B. pilularis, S. leucophylla*	8/1/2011	8/30/2011	193.97	6/6/2011

Table 2. Results of linear mixed effects model. Model selection based on AICc of principal components.

Species	Number of observations	Field sites	Model AIC			Model log-likelihood		
			PC1	PC2	PC3	PC1	PC2	PC3
A. californica	344	SSC1, SSC2, SSI	-1825.54	-1825.16	-1839.76*	917.77	917.58	924.88
A. fasciculatum	118	CHC	-749.14	-751.49*	-746.43	379.57	380.74	378.21
C. megacarpus	120	CHC	-765.31*	-762.66	-754.88	387.65	386.33	382.44
B. pilularis	349	SSC1, SSC2, SSI	-1821.47*	-1818.72	-1818.99	915.73	914.36	914.50
S. leucophylla	72	SSC1, SSI	-434.89	-436.47	-441.27*	222.44	223.23	225.64
C. cuneatus[%]	150	CHI	-894.88	-893.82	-899.33*	452.44	451.91	454.67

* indicates best model

[%] model does not include fog deposition or solar insolation

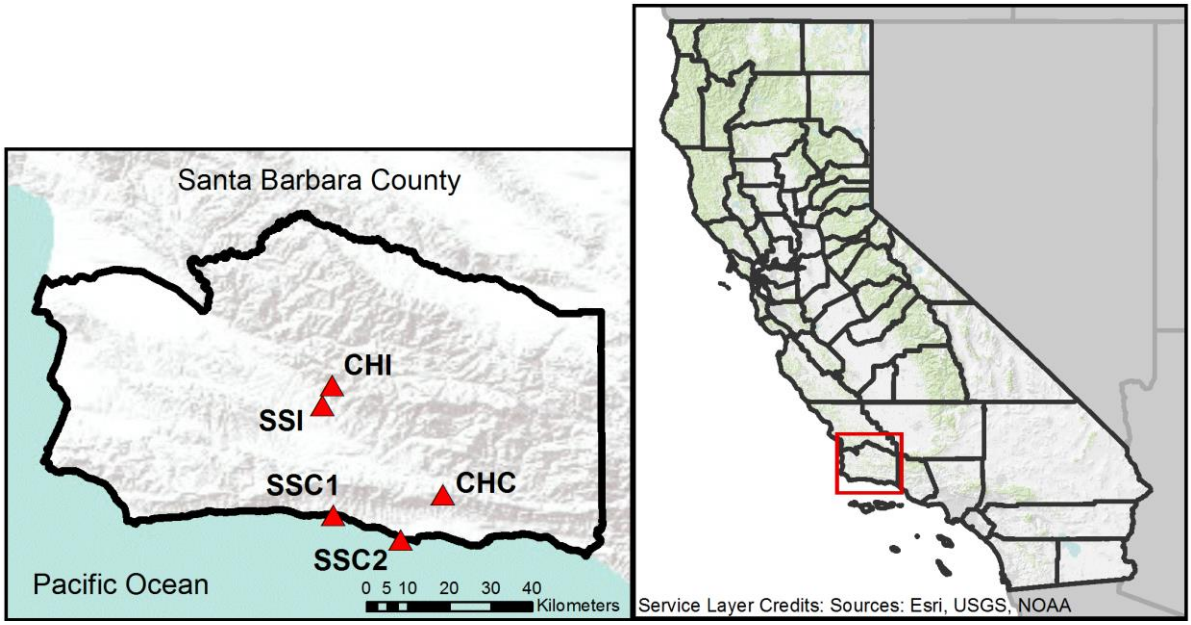

Figure 1. Map of field sites in Santa Barbara County, California. Sage scrub coastal species were measured at SSC1 in 2011 and SSC2 in 2012-2013.

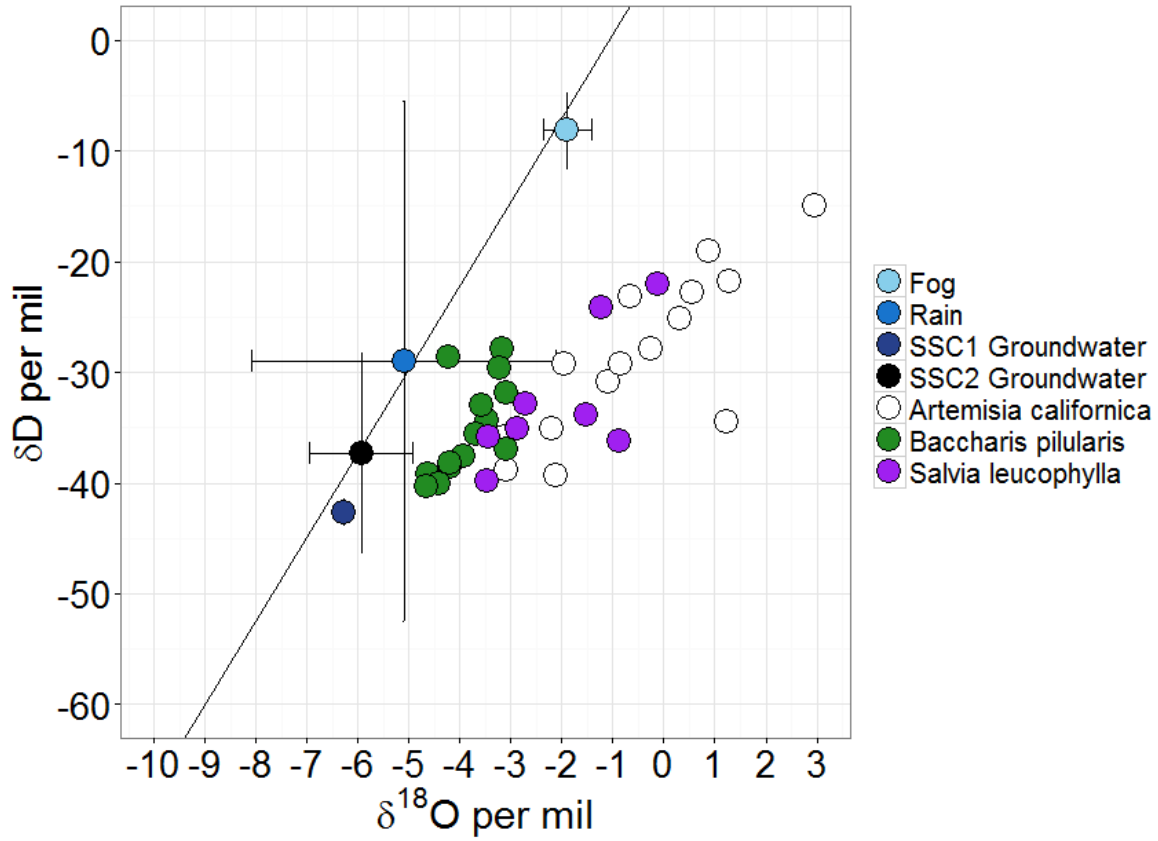

Figure 2. Isotopic ratios of water sources for the sage scrub coastal field sites (SSC1, SSC2). Each water source represents the volume-weighted average value from 2011-2013 (with standard error bars). The line represents the local meteoric water line (LMWL, slope of 7.57). Plant water samples fall to the right of the LMWL.

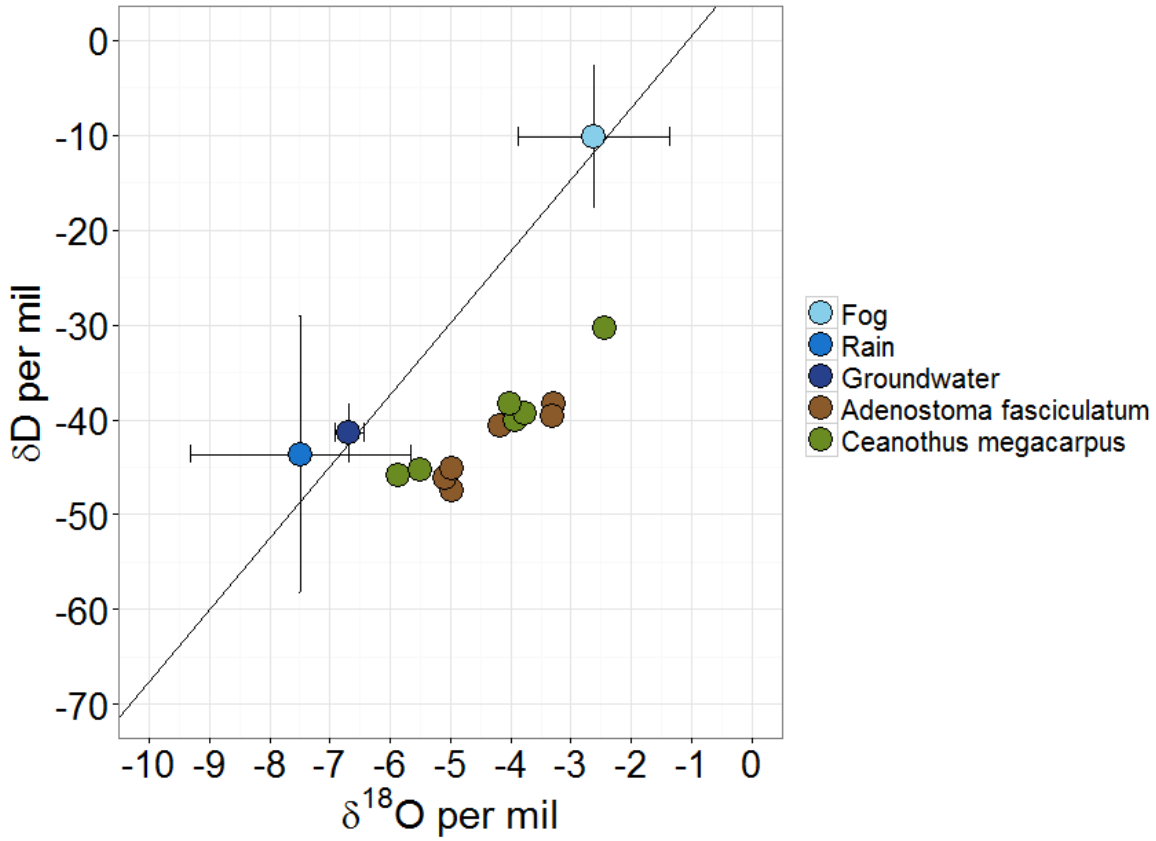

Figure 3. Isotopic ratios of water sources for the chaparral coastal field site (CHC). Each water source represents the volume-weighted average value from 2011-2013 (with standard error bars). The line represents the local meteoric water line (LMWL, slope of 7.57). Plant water samples fall to the right of the LMWL.

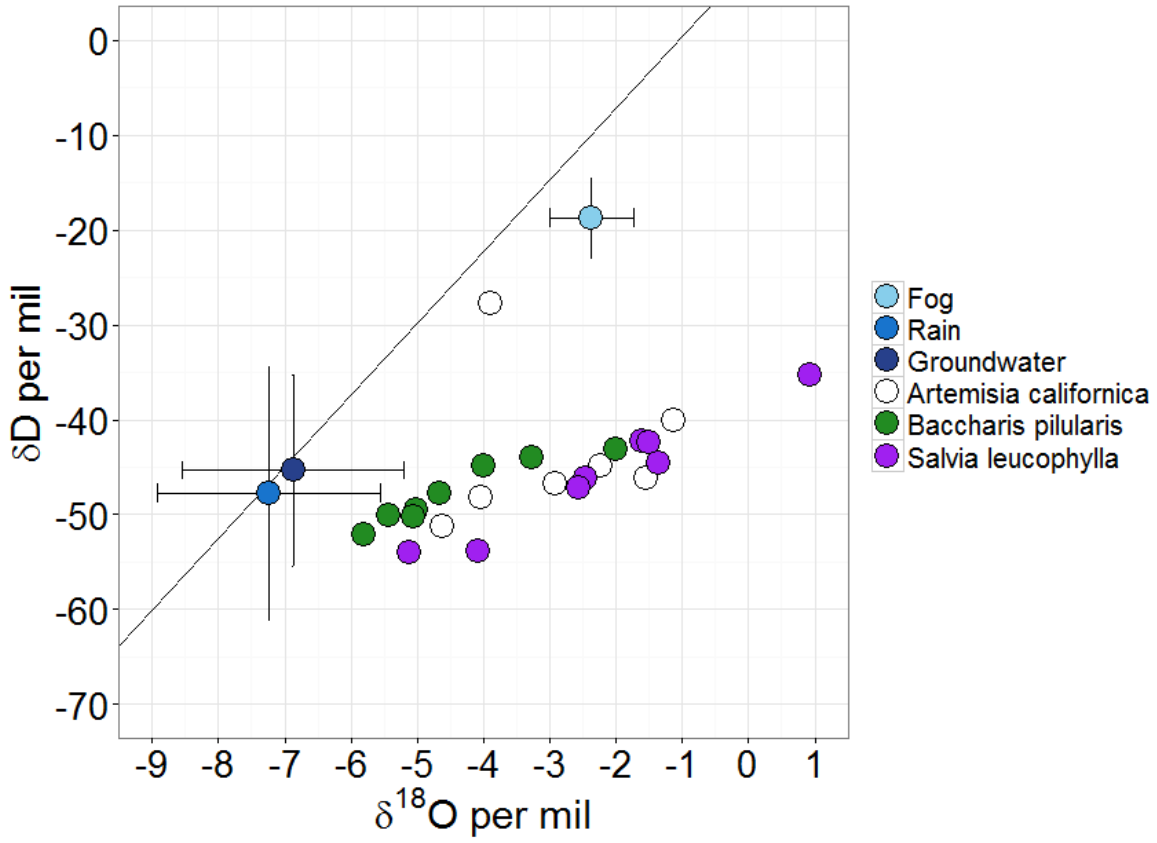

Figure 4. Isotopic ratios of water sources for the sage scrub interior field site (SSI). Each water source represents the volume-weighted average value from 2011-2013 (with standard error bars). The line represents the local meteoric water line (LMWL, slope of 7.57). Plant water samples fall to the right of the LMWL.

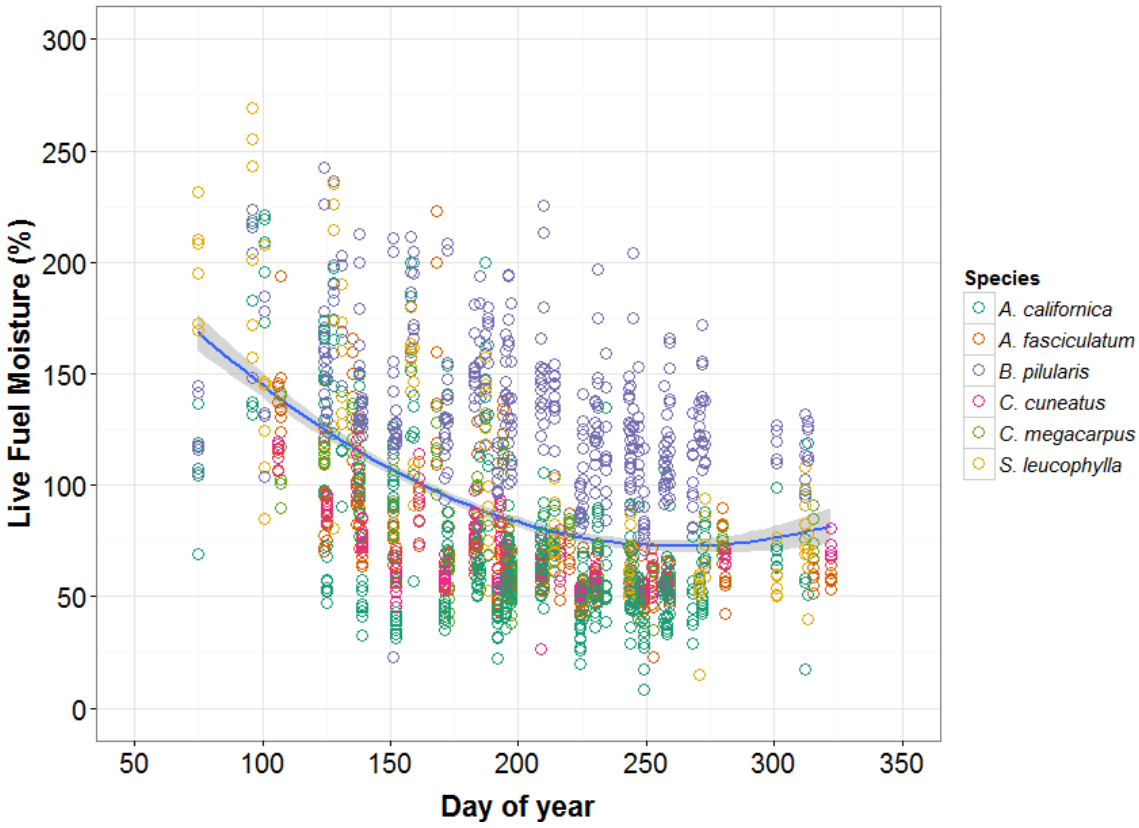

Figure 5. Live fuel moisture of all species over three summers (2011-2013) fitted with an exponential decay regression line and 95% confidence intervals. Each color represents a different species.

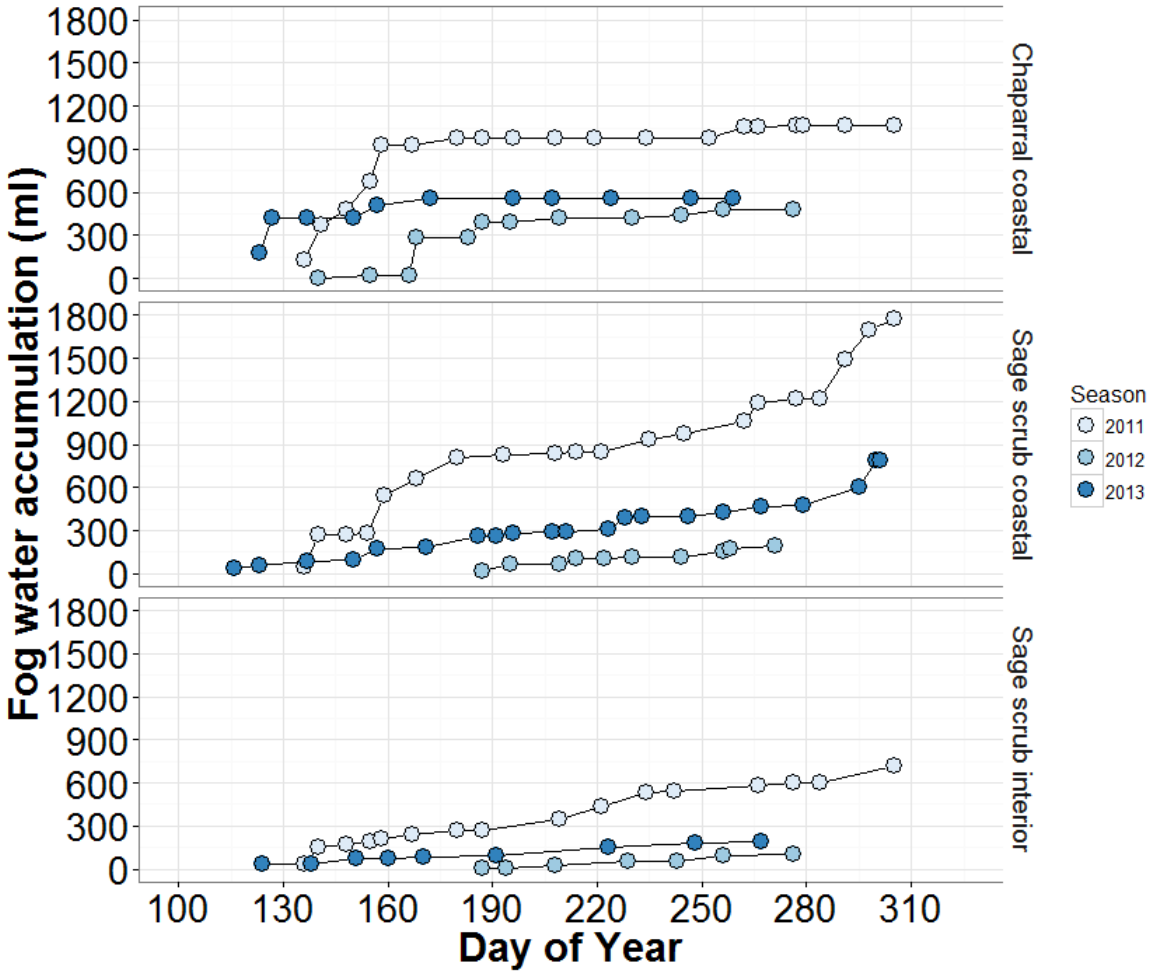

Figure 6. Fog deposition at CHC, SSC2 and SSI for the summers of 2011-2013. These data are the fog water accumulation over the summer months for a given year.

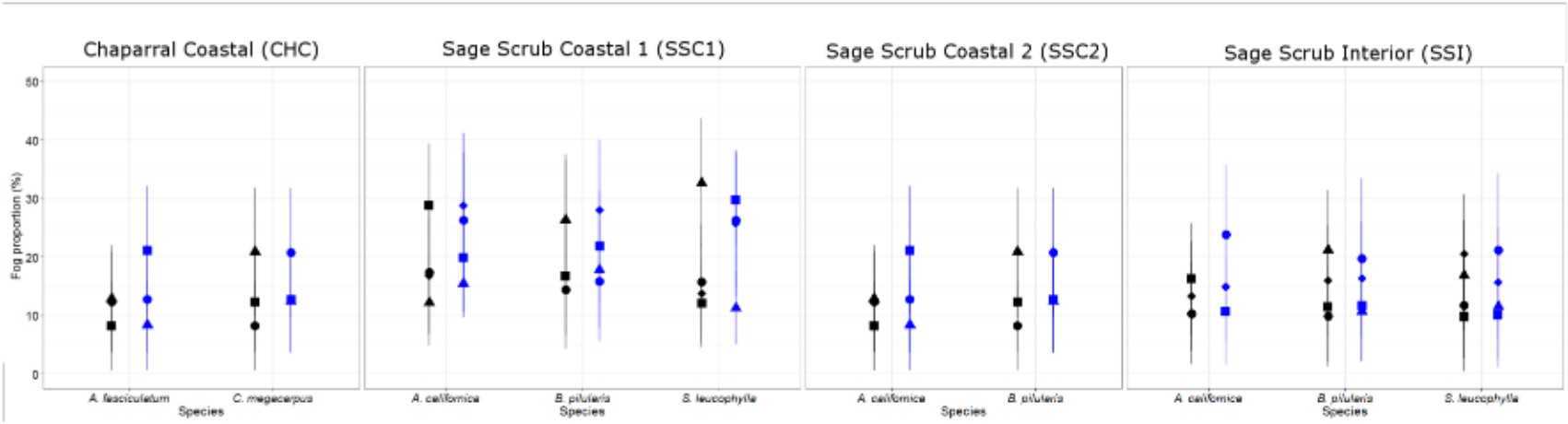

Figure 7. Proportional fog water uptake for all field sites. Pre-fog event samples are in black, post-fog in blue. Each shape represents the identification of a single shrub individual. The points and lines represent the mean and standard deviation output from the SIAR mixing model.

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APPENDIX I

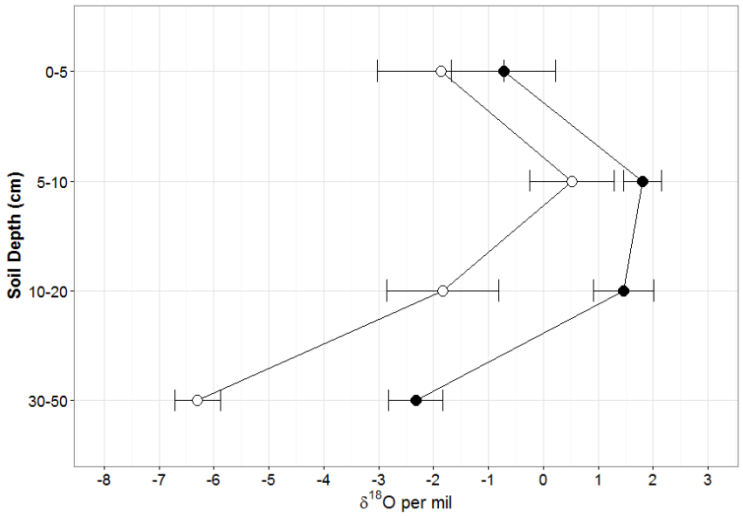

Figure A. Soil water oxygen isotope ratio values with depth for sage scrub coastal (SSC2, Black) and chaparral coastal (CHC, White) field sites. Points represent the mean value with standard error bars.

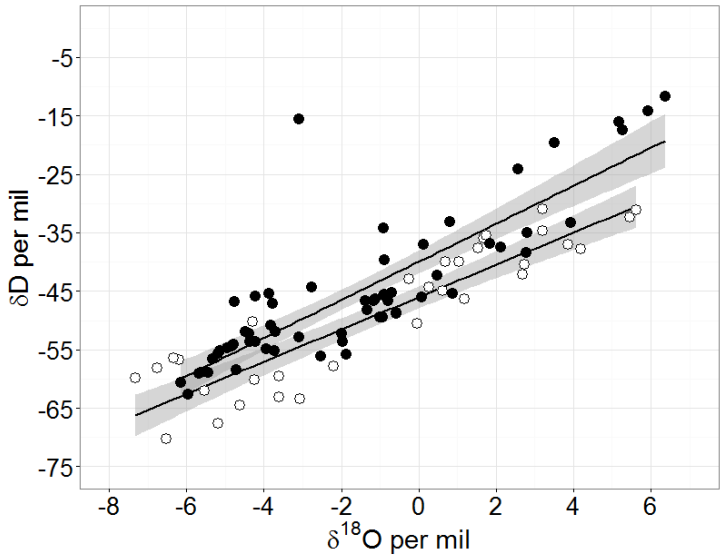

Figure B. Soil water evaporation fractionation with linear regressions for each plant association (SSC2 in black, CHC in white). The slope for SSC2 is 3.33 and the slope for

CHC is 2.76. The grey area represents the 95% confidence interval around each regression line.

The evaporation correction lines were developed using the methods detailed in Corbin et al. (2005). The slopes for the SSC2 and CHC field sites are comparable to the slope of 3.5 found by Corbin et al. (2005), slopes ranging from 2-5 for experimental soil water evaporative experiments using dune soils (Allison 1982) and a slope of 4.0 in a Mexican aquitard (Ortega-Guerrero et al. 1997). These three studies and the slopes found in this study are derived from non-saturated soils and lower than those resulting from saturated soils or open water bodies (Gonfiantini 1986, Barnes and Turner 1998). Variation in the slope is expected and to account for this, plant water samples were corrected using the slope and the 95% confidence interval of each slope before running the SIAR mixing model analysis. This resulted in a conservative estimate of proportional fog water in plant tissue for all study species.

APPENDIX II

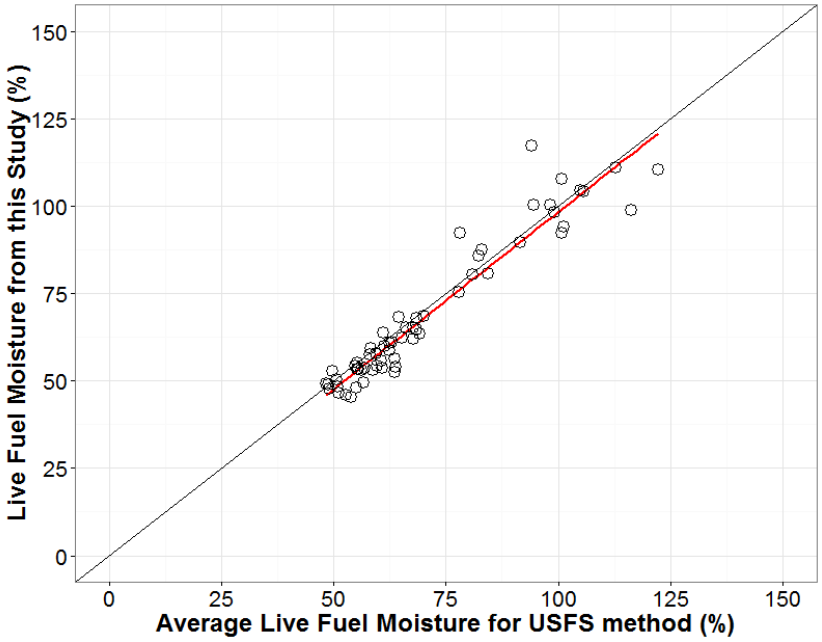

Figure A. Comparing the LFM method used in this study to the average of new and old LFM material sampled according to the USFS method for *A. fasciculatum* (Countryman and Dean 1979). The points represent paired samples from the same shrub individual. The black line is the 1 to 1 relationship between the two methods and the red line is a linear regression of the two methods ("LFM for this study" = 0.9065 * "Average LFM using the USFS method" + 0.0848, $r^2 = 0.9184$). This figure indicates that in *A. fasciculatum*, the LFM sampling method for this study is very similar to the average of new and old LFM using the USFS method.

APPENDIX III

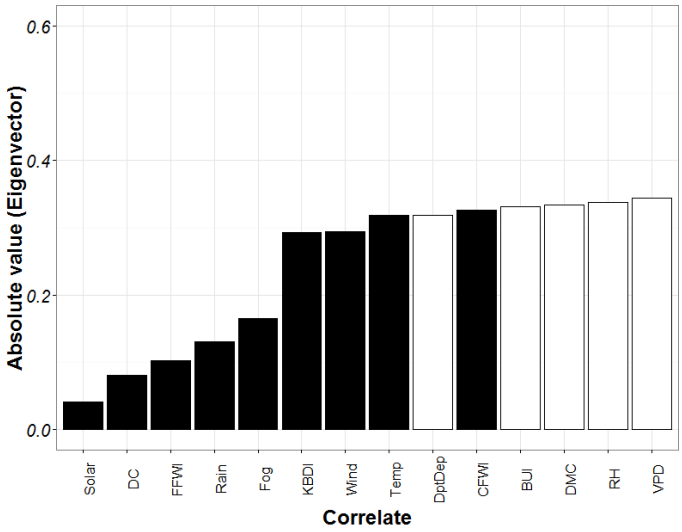

Figure A. Principal Component I loadings for field sites SSC1, SSC2, CHC and SSI. Black bars and white bars represent positive and negative eigenvectors respectively.

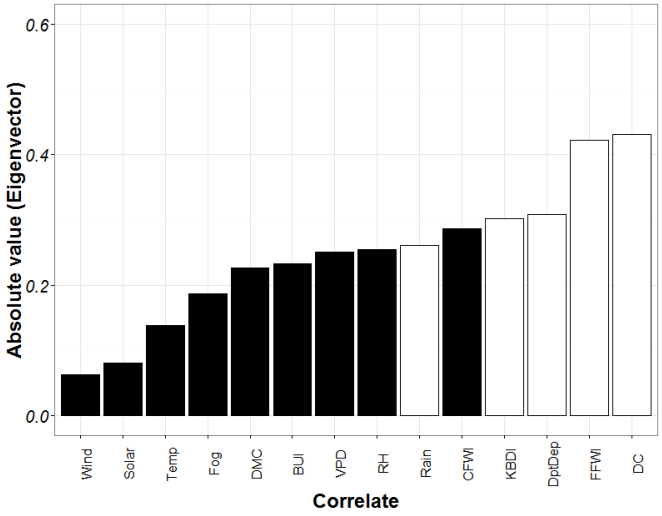

Figure B. Principal Component II loadings for field sites SSC1, SSC2, CHC and SSI. Black bars and white bars represent positive and negative eigenvectors respectively.

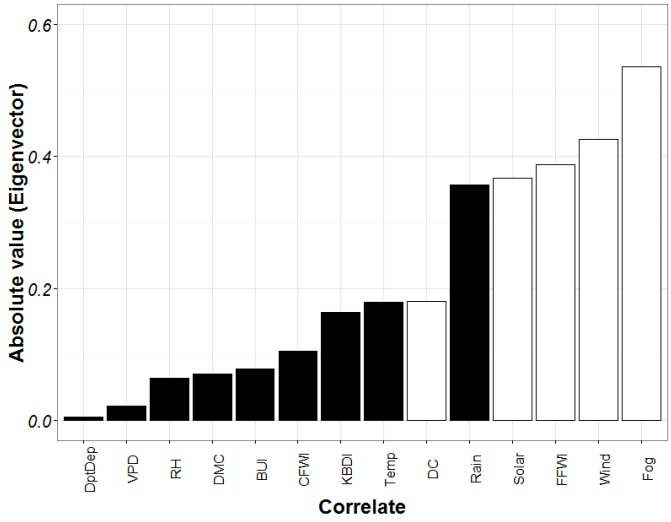

Figure C. Principal Component III loadings for field sites SSC1, SSC2, CHC and SSI. Black bars and white bars represent positive and negative eigenvectors respectively.

APPENDIX IV

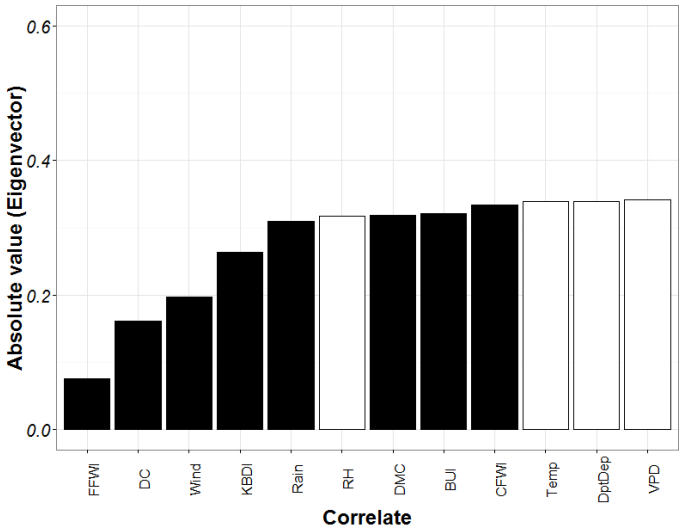

Figure A. Principal Component I loadings for field sites CHI. Black bars and white bars represent positive and negative eigenvectors respectively.

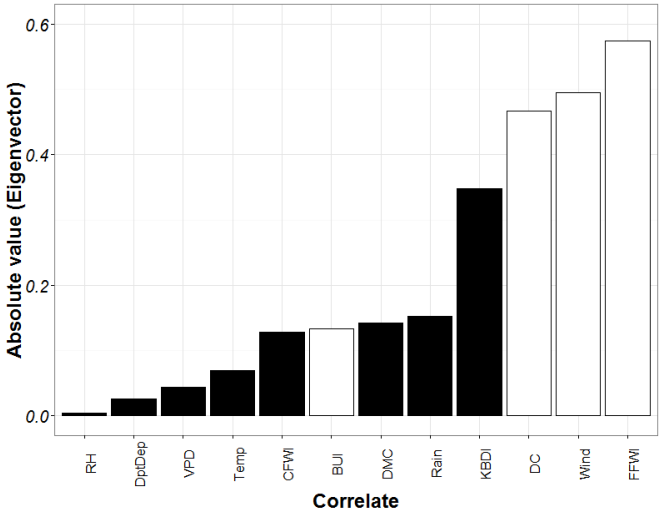

Figure B. Principal Component II loadings for field sites CHI. Black bars and white bars represent positive and negative eigenvectors respectively.

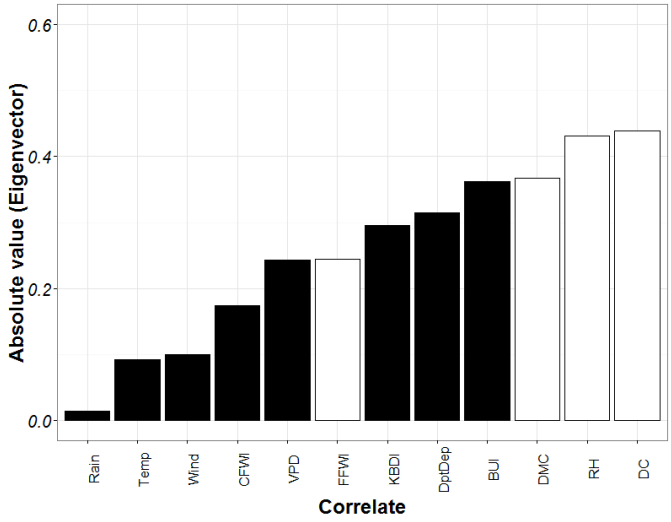

Figure C. Principal Component III loadings for field sites CHI. Black bars and white bars represent positive and negative eigenvectors respectively.

APPENDIX V

Meteorological indices and environmental correlates of live fuel moisture

Name	Code	Aggregation	Inputs	Reference
Temperature	*Temp*	2 week mean	n/a	n/a
Relative Humidity	*RH*	2 week mean	n/a	n/a
Wind	*Wind*	2 week mean	n/a	n/a
Vapor Pressure Deficit	*VPD*	2 week mean	Temp, RH	n/a
Dewpoint Depression	*DptDep*	2 week mean	Temp, RH	n/a
*Solar Insolation**	*Solar*	2 week sum	Pyranometer	n/a
Rain	*Rain*	2 week sum	Rain gauge	n/a
*Fog per day**	*Fog*	2 week mean	Fog collector	Fischer et al. 2007
Duff Moisture Code	*DMC*	2 week mean	Temp, RH, Rain	Lawson and Armitage 2008
Drought Code	*DC*	2 week mean	Temp, Rain	Lawson and Armitage 2008
Build-Up Index	*BUI*	2 week mean	DC, DMC	Lawson and Armitage 2008
Canadian Fire Weather Index	*CFWI*	2 week mean	Temp, RH, Rain, Wind	Lawson and Armitage 2008
Keetch-Byram Drought Index	*KBDI*	2 week mean	Rain, Temp	Keetch and Byram 1968
Fosberg Fire Weather Index	*FFWI*	2 week mean	Temp, RH, Wind	Fosberg 1978

* not available for CHI

Mean temperature, relative humidity and vapor pressure deficit were used in the model instead of maximums and minimums because all three were correlated within each metric. The indices and environmental factors were aggregated over two weeks prior to each date of the study. These correlates were decomposed into principal components for the field sites SSC1, SSC2, CHC and SSI. A separate PCA was performed for the CHI field site as no solar insolation or fog deposition data was available.